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THE CYST-FORMING SPECIES OF HETERODERA

by

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PREFACE

The genus *Heterodera* of the Family Tylenchidae in the Class Nematoda comprises the root-knot nematode *Heterodera marioni* and the cyst-forming species formerly known as the single species *H. schachtii* Schmidt, 1871, and now divided into a number of species. Because of the economic importance of attacks on agricultural crops by cyst-forming *Heterodera* spp., there has been a considerable amount of research on various aspects of their biology and control, the published accounts of this work being widely scattered and in half-a-dozen languages. The comparatively recent splitting of the species *H. schachtii* and the scattered nature of the literature on the subject prompted the idea that the bringing together of all the known information about the species would serve a useful purpose in guiding future work on the genus. This publication, then, is a review of most of the published work on the cyst-forming species of *Heterodera* up to the end of the year 1948 ; a considerable number of new observations are included. The bibliography is as complete as possible : those papers which it has not been possible to see are marked with an asterisk. A great deal of the bibliographic work has been done at the Commonwealth Bureau of Agricultural Parasitology, St. Albans.

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CHAPTER I

THE GENUS *HETERODERA* SCHMIDT, 1871

The genus *Heterodera* forms a group of about a dozen species of nematodes, all of which are parasitic on the roots and underground stems of vascular plants. Many of the principal crops in cultivation may be seriously affected by these parasites, which have in consequence been studied largely in relation to the damage caused by them to their hosts. Their activities within the host roots result in disturbances in the translocation of the plant nutrients with a reduction in the amount of food available for growth, and consequent weak development of the plant. One species, *H. marioni*, the root-knot nematode, stands somewhat apart from the rest. It gives rise to severe galling of the roots of most of the plants which it attacks. This species, or possibly group of species, has no very resistant stage in its life-history, but is afforded some protection from adverse soil conditions such as drought or absence of host plants by the galled tissues of the root in which it has developed. All the other species are characterized by the transformation of the body wall of the adult female into a tough resistant cyst or sac containing the embryonated eggs which, thus protected, remain viable for a number of years in the soil. These cyst-forming species are characteristic of the more temperate regions of the world, while root-knot nematodes occur chiefly in tropical and subtropical regions, although they are also found occasionally in colder climates, both in the open and in greenhouses. On account of its differences from the cyst-forming species of *Heterodera*, *H. marioni* is mentioned in this paper only in a general way.

Historical Introduction

The type species of the genus *Heterodera* is *H. schachtii*, the sugar-beet eelworm, described in 1871 by A. Schmidt. The root-knot eelworm (*H. marioni*) was, however, the first to be mentioned in the

literature ; it was discovered by Berkeley in 1855, causing galls on the roots of cucumbers in an English greenhouse, and referred to as a " vibrio ". In 1884 Müller[1] found worms in galls on the roots of *Dodartia orientalis*, and recognized that they belonged to the genus *Heterodera*. He mistakenly took them to be the same as those described by Greeff[2] in 1872 as *Anguillulina radicicola*, and called them *Heterodera radicicola*. However, in 1932 Goodey[3] pointed out the error, and the root-knot nematode is now known as *H. marioni* (Cornu, 1879) Goodey, 1932. Recent work has shown that there may be biological races or even species of *H. marioni*, differing in their host preferences (Christie & Albin, 1944[4] ; Christie, 1946[5] ; Chitwood, 1949[6]).

H. schachtii was first found infesting the roots of sugar-beet by Schacht in 1859, and within the following ten to twenty years it became recognized as a pest of great importance in the beet-growing areas of Germany, France (Girard, 1884), Finland (Warming, 1879) and Holland (Chatin, 1887).

From the time of the earliest investigators, there was evidence for the existence of at least two distinct races within the species. The nematode was well known throughout Europe as a pest of sugar-beet from 1860 onwards (Schacht, 1861b), and it was also known to attack turnip, rape and other brassicas. At about the same time a closely similar parasite was observed on the roots of oats, barley and wheat (Kühn, 1874), and rye was found to be susceptible (Kühn, 1881), although to a lesser degree. The race attacking cereals was soon recognized as distinct from that attacking sugar-beet, and was referred to by Danish workers from 1908 onwards (Mortensen, Rostrup & Kølpin Ravn, 1908) as *H. schachtii* var. *avenae*. In 1930 O. Schmidt described it and, considering it to be of subspecific rank, called it *H. schachtii* subsp. *major*.

[1] Müller, C., 1884.—" Mittheilungen über die unseren Kulturpflanzen schädlichen, das Geschlecht *Heterodera* bildenden Würmer." *Landw. Jb.*, **13** (1), 1–42.

[2] Greeff, R., 1872.– "Ueber Nematoden in Wurzelanschwellungen (Gallen) verschiedener Pflanzen." *S.B. Ges. ges. Naturw. Marburg*, pp. 169–174.

[3] Goodey, T., 1932. "On the nomenclature of the root-gall nematodes." *J. Helminth.*, **10** (1), 21–28. [Helm. Abs., **1**, No. 17c.]

[4] Christie, J. R. & Albin, F. E., 1944. " Host-parasite relationships of the root-knot nematode, *Heterodera marioni*. I. The question of races." *Proc. helminth. Soc. Wash.*, **11** (1), 31–37. [Helm. Abs., **13**, No. 55j.]

[5] Christie, J. R., 1946. " Host parasite relationships of the root knot nematode, *Heterodera marioni*. II. Some effects of the host on the parasite." *Phytopathology*, **36** (5), 340–352. [Helm. Abs., **15**, No. 47c.]

[6] Chitwood, B. G., 1949.—" ' Root-knot nematodes '—Part I. A revision of the genus *Meloidogyne* Goeldi, 1887." *Proc. helminth. Soc. Wash.*, **16** (2), 90–104. [Helm. Abs., **18**, No. 254d.]

It was raised to the rank of a species under the name of *H. major* in 1940 (Franklin, 1940c).

Another race of *H. schachtii* was recognized by Liebscher in 1890 as being especially adapted to peas, beans and vetches. He found it established at Göttingen, where it was causing considerable damage to peas. As it was unable to live on sugar-beet or on cereals, and had certain morphological differences from the races parasitic on these plants, Liebscher considered it to be of specific rank, and named it *H. göttingiana*. Since 1890 the pea root eelworm has been found damaging peas, beans and vetches in France and Germany and in many parts of England and Wales.

The most destructive of all the root eelworms in Britain is the potato root eelworm, now known as *H. rostochiensis*. The potato was often classified in the past amongst the plants not attacked by *Heterodera*, e.g. by Hollrung (1890a), and by Vaňha & Stoklasa (1896). But Kühn (1881) and Marcinowski (1909) both stated that the potato was susceptible, and in 1913 Massee reported that in Scotland it was seriously damaged by this nematode. Since then potato root eelworm has grown in importance all over Britain and the continent of Europe, and in 1941 (Cannon) it was first reported in the U.S.A. At first it was considered to be a biologic race of *H. schachtii* which had become especially adapted to potatoes, but Wollenweber in 1923 recognized morphological differences between the cysts formed on potatoes and those on sugar-beet, and named the potato root eelworm *H. rostochiensis*.

These five species of *Heterodera—H. marioni, H. schachtii, H. major, H. göttingiana* and *H. rostochiensis*—are economically the most important members of the genus so far known. However, at least seven other cyst-forming species and varieties are now recognized, and although the damage caused by them to crop plants has so far been slight, they are potentially dangerous pests.

The species and varieties not so far mentioned are : *H. cacti* (Filipjev & Schuurmans Stekhoven, 1941), *H. cruciferae* (Franklin, 1945), *H. humuli* (Filipjev, 1934), *H. punctata* (Thorne, 1928b), *H. schachtii* var. *galeopsidis* (Goffart, 1936c), and *H. schachtii* var. *trifolii* (Goffart, 1932a). Two additional species have recently been described, *H. weissi* on polygonum in the U.S.A. by Steiner (*Proc. Soil Sci. Soc. Fla*, 1949 (Year 1942), **4**B, p. 99 ; mentioned also by Steiner, 1947 and by Cunningham & Mai, 1947), and *H. carotae* on carrots in England by Jones (*Nature, Lond.*, 1950, **165** (4185), 81). In addition, a race attacking soya beans in Japan may prove to be a definite species (Ito, 1921 ; Fujita & Miura, 1934).

Morphological Characters of the Genus

Whilst the males are worm-like, 1.0–1.5 mm. long, the mature females are swollen and flask-shaped, with a short appendage formed by the head and neck at the anterior end, and when mature are visible to the naked eye. When the female dies the body wall hardens and becomes a sac for the eggs, usually several hundred in number, in each of which a coiled larva eventually develops.

In all stages, the lip region is slightly constricted from the body and has six radial ridges marking the position of the fused lips. There are several transverse striations or annulations on the head, the number apparently differing in the different species, but the variations have not yet been thoroughly worked out. The cuticle throughout the length of the body is also marked with transverse striations, and lateral fields are present. The mouth stylet, varying in the different species from 10μ to 33μ long, is in two parts, an anterior conical part and a posterior cylindrical part bearing three basal knobs. The mouth opening is pore-like and leads to a tubular buccal cavity, in the walls of which are cuticularized areas which serve to guide the stylet as it is pushed out and withdrawn. There is a median, rounded, muscular oesophageal bulb with cuticularized plates in the walls. The intestine is a straight tube running the length of the body to end in a short rectum and an anus opening a little way in front of the body terminus. Three uninucleate oesophageal glands lie in a row obliquely ventrally or ventro-laterally to the anterior part of the intestine; the anterior dorsal one opens by a duct into the oesophagus just behind the base of the stylet, the other two into the muscular bulb just behind the cuticular plates. The nerve ring encircles the oesophagus behind the muscular bulb, and the excretory pore opens ventrally close behind the nerve ring.

Male.—There is considerable variation in the size of the males, even in the same species, but usually they vary between 1.0 mm. and 1.5 mm. in length. The tail is short and bluntly rounded, without caudal alae, and the phasmids are extremely minute. The gonad is single. There is a pair of curved spicules considered to be copulatory in function, and about 25μ long; they diverge anteriorly and each is made up of a somewhat stout anterior portion resembling a handle, with a curved posterior part tapering to a point which varies in form in the different species of the genus. The posterior part has various longitudinal ribs, and the edges appear in some cases to be rolled ventrally. There is a small simple gubernaculum.

In some species the cuticle in the region of the tail appears to be slightly expanded laterally, but there is no bursa.

Female.—In the mature female little can be seen but the reproductive organs, consisting of paired ovaries with oviducts, receptacula seminis and uteri leading to a common vagina which opens at a terminal vulva. The minute anus is just dorsal to the vulva. In some species a gelatinous exudate of varying amount is attached to the vulva, forming a kind of egg-sac. In mature females of some species this is packed tightly with eggs, and may also contain several males ; in other species, eggs in the sac are few or absent. The body wall is thickened and eventually becomes brown and tough in the dead worm in the cyst-forming species, in contrast to *H. marioni* where it remains white and is comparatively easily ruptured. In some species the cyst is more or less coated with a white incrustation which readily flakes off, known from its appearance as the subcrystalline layer.

Eggs.—These are oblong with rounded ends, in some species inclined to be barrel-shaped, but with slightly concave sides in others. The embryonated larva can be seen coiled up inside the transparent egg membrane. There is some variation in size and shape between the eggs of the various species. The smallest are those of *H. humuli* ($89\mu \times 42\mu$) and *H. cruciferae* ($94\mu \times 47\mu$), and the largest those of *H. punctata* ($122\mu \times 48\mu$) and *H. major* ($115\mu \times 49\mu$), while in the other species they are about 100–105μ long and 45μ broad. *H. göttingiana* differs from the other species in that the egg is broader both actually and relatively to its length, averaging $102\mu \times 54\mu$.

Larvae.—These have the general characters mentioned above, the head being only slightly offset from the gently tapering neck region, and the tail being sharply pointed. The transverse striations and lateral fields are fairly well marked. The length varies in the different species ; most of the known species can be grouped into one of three classes containing long, medium or short larvae respectively. The species *H. major* and *H. punctata* have long larvae of over 550μ ; *H. cruciferae*, *H. weissi* and *H. humuli* have short larvae, under 450μ long, while the other species have larvae of intermediate length ; *H. marioni* and *H. carotae* are on the border line with larvae 400-500μ in length.

Life-History

All the known species of *Heterodera* are obligate parasites, feeding and living for most of their lives in the roots of vascular plants. The eggs are released into the soil surrounding the host roots, either within the protective cyst formed by the body wall of the dead female, in a gelatinous egg-sac, or (*H. marioni*) in the decaying gall tissues of the host. The larvae remain dormant in the soil until the required stimulus is received, when they hatch from the eggs and emerge from the cyst, egg-sac or decaying gall into the surrounding soil, and make their way to a suitable plant root. Their movements in water are comparatively sluggish, and little is known of their rate of progress in the soil or of the means by which they find the host root, but it is known that they are capable of survival in the soil for at least several weeks, and probably for several months under favourable conditions. While free in the soil they do not feed, and it is thought that they are attracted chemotropically to a suitable host root. When they have reached the host rootlet, they enter at the growing region immediately behind the root tip and make their way through the cortex to the pericycle surrounding the central vascular tissue. Here they establish themselves, usually lying longitudinally with head pointing away from the root tip, and begin to feed and develop. The rate of development varies with the temperature, the host plant and the species of eelworm concerned; it is usually completed in four to six weeks, when three or four moults have occurred.

In *H. marioni* the first moult takes place in the egg[1], and it is the second-stage larva which hatches and invades the host root; there, three further moults occur before the adult stage is reached. In *H. rostochiensis* all four moults take place within the host root, which is invaded by the first-stage larva (Chitwood & Buhrer, 1946a). With the exception of the root-knot eelworm, in which the parasites are usually buried in the galls of the host root, the mature male and female nematodes can be seen on the surface of the roots, the male as a small white sausage-shaped sac within which the worm is at first coiled, but from which it soon emerges to wander in the soil in search of the female; the latter is swollen and pear-shaped or spherical, and lies on the surface of the root, attached by the neck which is still inserted in the root. Fertilization probably takes place

[1] Christie, J. R. & Cobb, G. S., 1941.—"Notes on the life history of the root-knot nematode, *Heterodera marioni*." *Proc. helminth. Soc. Wash.*, **8** (1), 23–26. [Helm. Abs., **10**, No. 36j.]

at this stage, and after a short period of further wandering in the soil the male dies. The female continues to feed for a time and the eggs develop inside her, finally occupying the whole of the body so that all other organs are completely obliterated. Segmentation of the eggs begins at once, and the first embryos may be seen within a week or two of fertilization. The body wall of the female then becomes thickened and tough, turning brown as the worm dies, and is transformed into a cyst. The gelatinous egg-sac, when present, is produced before the cyst turns brown. An egg-sac is found in *H. marioni*, but the female body wall remains white and comparatively thin. In some species it is not unusual to find one or more males trapped in the gelatinous egg-sac, and apparently dead.

In *H. marioni* the eggs usually hatch soon after they are embryonated, and there may therefore be several generations in one season. In the cyst-forming species many of the eggs do not hatch in the same year in which they are formed, so that few or only one generation occurs annually. The larvae may remain dormant but viable within the cyst for several years, possibly ten or more, and may still be able to hatch when a suitable host plant is present. Thus the starving-out of the parasite from an infested soil is a very lengthy process in the cyst-forming species, whereas in the case of *H. marioni* it can be achieved in a few months or a year in the absence of host plants.

Effect on Host

The invasion of a rootlet by large numbers of *Heterodera* larvae may result in the death of the rootlet, either from direct injury or as a result of secondary invasion of the damaged tissues by fungi or bacteria from the soil. If few larvae enter a root the tissues are not killed; on the contrary they are often stimulated, and new side roots quickly develop at or near the points where the larvae settle. (In the case of attack by *H. marioni* the cortical cells proliferate and form galls of paranchymatous tissue, which may become several times as great in diameter as the original root.) In addition to these macroscopic developments, certain cells in contact with the head of the feeding nematode become greatly enlarged and develop granular contents; they are usually referred to as "giant cells". The eelworms lie between the cells, the middle lamellae of the walls breaking down so that the cells separate from one another. The general effect of these changes within the host roots is, by disturbing the system of translocation, to interfere with the nutrition of the plant. This may produce no noticeable signs in the

parts above ground, or may lead to an unhealthy, stunted appearance. The extent to which actual disease of the plant occurs depends on climatic and biological factors acting on the host at the same time as the parasites, but independently of them.

CHAPTER II

HETERODERA SCHACHTII SCHMIDT, 1871

THE SUGAR-BEET EELWORM

Syn. *Tylenchus schachtii* (Schmidt, 1871) Oerley, 1880
Heterodera schachtii subsp. *minor* O. Schmidt, 1930

Since it was the first member of the genus *Heterodera* to be recognized as an important pest of agricultural crops, the sugar-beet eelworm, from its original discovery by Schacht (1859a,b) up to the present day, has been studied intensively from several angles in various parts of the world. A very valuable account of the work published during the first fifty-five years after its discovery was given by Shaw (1915). Since then most investigations have been directed towards its control, but its host range has also been studied extensively. However, since what used to be thought a single species is now known to comprise several species and strains, the earlier host lists of *H. schachtii* cannot be considered valid for the species as it is recognized at the present time. The original studies on the morphology and life-history of the nematode were carried out on specimens obtained from the roots of sugar-beet, and there is therefore little doubt but that they apply to *H. schachtii* (*sensu stricto*).

Morphology

Male.—Very variable figures have been given for the length of the male of *H. schachtii*. Triffitt (1929c) measured males from sugar-beet plants and gave the following dimensions: length 1.32–1.63 mm. with an average of 1.46 mm., and an average ratio of length to breadth of 37 to 1; stylet 28μ and spicules 34μ in length. She found that males from mangolds were 1.22–1.59 mm. long, averaging 1.42 mm., with a ratio of length to breadth of 43 to 1; stylet 27.9μ and spicules 34.6μ long. These measurements are

very similar, but Strubell (1888) gives the average length of males from beet as 0.8-0.9 mm. and the length breadth ratio as 32 to 1, with a stylet 30μ and spicules 33μ long. Marcinowski (1909), on the other hand, gives the ratio of length to breadth as 48 to 1. Differences in the published figures may be due to differences in the methods of measuring or fixing the worms. It is probably true to state that the average length of males of the sugar-beet eelworm is about 1.5 mm., and the ratio of length to greatest breadth is approximately 40 to 1 [Fig. 1 (1)].

The head region is slightly constricted from the rest of the body, and is marked by three or four annular striations. The fused lips and skeletal structures are typical of the genus (Fig. 1 (2)).

The copulatory spicules are characterized by being fairly broad at the tip, which is bidentate (Fig. 1 (1)). The gubernaculum is small. There are rather inconspicuous lateral wing-like expansions of the cuticle in the region of the spicules (Triffitt, 1928), but nothing approaching a bursa.

Female.—The mature female is distinctly lemon-shaped, the body being ovoid with a short neck anteriorly and a prominent knob-like vulva posteriorly (Fig. 3 (4)). A well marked sub-crystalline layer coats the newly formed cyst, but is soon lost when the cyst becomes loose in the soil. The female is white when she first bursts through the host root, but after fertilization, as the eggs develop and the worm dies, the body wall becomes a light brown and gradually darkens to a medium brown, while the wall itself becomes tough and resistant to drying. There is often a gelatinous mass attached to the vulva while the cyst is still in position on the host root; it may be about one-third the size of the cyst, and sometimes contains a few eggs, especially in the case of the larger cysts (Fig. 3 (3)).

The size of the cysts of the sugar-beet eelworm is very variable. Goffart (1930a) gives the mean body length, excluding the neck, as being 652μ for cysts from a population parasitizing sugar-beet in Germany. The width of the cysts averaged 466μ, and the ratio of length to breadth was 1.4 to 1. For cysts growing on mangolds, Triffitt found the mean length to be 763μ and the width 510μ, giving a length to breadth ratio for cysts from mangolds of 1.476 to 1. It is thus apparent that the actual size of the cysts may vary considerably, but that as a rule they are about 0.6–0.7 mm. long and about 1.5 times as long as broad.

The mouth stylet of the female is somewhat smaller than that

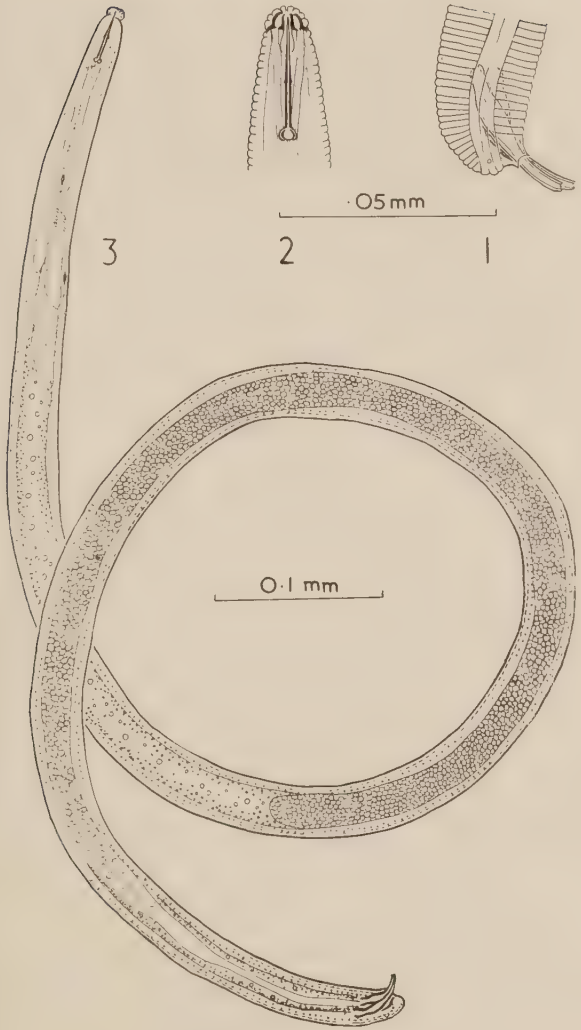


FIG. 1.—*Heterodera schachtii*. (1) Tail of male showing bidentate tips of spicules. (2) Head. (3) Male [orig.].

of the male, measuring 22–26μ in a few specimens from mangolds (writer's observation).

Sometimes, when a mature white female is forcibly removed from the root where she is feeding, one or two drops of fluid will be found in the region of the mouth. These harden in a short time and turn dark brown. They were said by Shaw (1915) to be derived from the sap of the sugar-beet on which the animal is feeding. They are, however, more like the tough brown knobs which occur inside the cyst surrounding the vulval aperture. Similar hardened droplets are sometimes seen on the neck of cysts of other species of *Heterodera*.

If the surface of the cyst wall is examined under the microscope, it will be seen to be covered uniformly with very minute translucent spots. These are the so-called "punctations", and in *H. schachtii* they are arranged irregularly, though evenly disposed over the entire cyst wall. They appear to be superficial sculpturings.

Eggs.—A mature cyst may contain several hundred eggs, the number varying according to the size of the cyst. Triffitt (1929c) gives the average size of an egg as 114μ × 45μ from sugar-beet and 112μ × 46μ from mangold. Goffart (1930a) gives the size of eggs from sugar-beet as 102.8μ × 42.9μ. In shape they are oblong with rounded ends and fairly straight sides, though the shape varies a little according to the side from which they are observed.

Larvae.—The larvae are of medium length as compared with those of other members of the genus; they may vary slightly with the host on which they develop. On sugar-beet they are 457μ and 447μ according to Triffitt (1929c) and Goffart (1930a) respectively, while from mangolds Triffitt found them to be 500μ long, and Franklin (1945) 475μ. Franklin also measured larvae of this species from radish and cabbage, and found the lengths to be 463μ and 459μ respectively.

The mouth stylet is usually 24–25μ long and fairly stout. The cuticular striations are fairly well marked and the tail is pointed.

Bionomics†

Cysts removed from a soil having an infestation of sugar-beet eelworm of several years' standing contain very variable numbers of embryonated eggs. While some cysts are full and others empty, a a large number contain both unhatched embryos and empty egg membranes. This is because the larvae do not all hatch from a cyst

† See also Raski, D. J., 1950, *Phytopathology*, **40** (2), 135-152.

in one season, but over a number of years. It was shown by Baunacke (1922a) and by Rensch (1924) in laboratory experiments that while a few larvae will emerge from cysts kept in plain water, very many more will hatch in water which has been in contact with the roots of a host plant such as mangold, sugar-beet or rape. It is probable that in the field the larvae hatch in large numbers only when stimulated by substances produced by the growing roots of certain plants (formerly referred to as root " excretions " but now usually as root " diffusates "), or in the presence of certain chemicals.

Temperature also affects the hatching of the larvae from the cysts. According to Baunacke (1922a), some larvae hatch at 16°–18° C., but 25° C. is the optimum temperature for hatching. Moisture and oxygen also have some effect. Triffitt (1930a) showed that the larvae of *H. rostochiensis* will not hatch in the absence of oxygen, and it is probable that the same applies to *H. schachtii*.

The larvae emerge from the cyst either through the vulva or by way of the neck and oral aperture, and move about in the soil until they find a suitable plant root. They can probably survive for some months in the soil. According to Nebel (1926a) they may live for two years, though it is very probable that they do not feed until they enter the host root.

The penetration of the plant root is probably achieved with the aid of the mouth spear. The method of entry and of feeding within the root have been studied by Berliner & Busch (1914), Sengbusch (1927) & Němec (1911, 1933). Berliner & Busch studied the larvae in agar and came to the conclusion that they could only enter roots through injuries, but Němec considered that the mouth spear was used in forcing an entry, and he saw worms making repeated thrusts with it. Linford (1941)[1] observed the entry of larvae of *H. marioni* into plant roots ; he saw the worms making repeated thrusts with the mouth spear until eventually a hole was pierced in the cell wall through which a larva could enter. It seems probable that the sugar-beet eelworm enters in the same way. The root is usually attacked in the region just behind the tip, and the larva takes up its position with its head adjoining the cells of the pericycle, lying parallel with the vascular cylinder, its tail pointing towards the root tip. Sengbusch describes how the larva travels in the root :

[1] Linford, M. B., 1941.—" The feeding of nematodes before and during their entry into roots." *Phytopathology*, **31** (9), 862. [Helm. Abs., **10**, No. 168e.]

he says that when it reaches a cell wall it uses the stylet to make a perforation, then pushes against the perforated area until it bursts through into the cell beyond. In this way it traverses the cortex until it reaches the edge of the vascular cylinder. According to Sengbusch, the feeding larva perforates the wall of an adjacent cell with its mouth spear, and through the perforation protrudes from its mouth a tube-like structure, through which, he presumes, it sucks out the cell contents. It seems likely that this apparent tube is in reality a fluid of a salivary nature injected into the cell by the larva, as is the case in *H. marioni*, according to Linford. In spite of the opinion of Němec (1933) that the larva does not perforate the walls of the cell surrounding its head, it seems probable that it does actually pierce the wall with its stylet, but that the perforations contract so as to be invisible when the spear is withdrawn, though a sufficiently large pore is left for some of the contents of the cell to be exuded and absorbed as food material by the parasite. Whether or not this is the exact process by which the nematode feeds, it is certain that the cells nearest its head become much enlarged and develop granular contents. Several adjacent cells coalesce to form one large "giant cell" or syncytium with several nuclei. As these giant cells enlarge they interfere with the conducting strands of the root, sometimes blocking the veins and so reducing the flow of nutrients to the growing parts of the plant. The form and development of giant cells have been described by Němec (1933), who likened them to nectaries.

A few days after it has taken up its permanent position in the root the larva undergoes its first moult, without much alteration in size. It continues to feed and a week or ten days later the second moult occurs, by which time it has increased in girth but has changed little in length. Growth continues, and soon the males can be distinguished from the females by their cylindrical shape as compared with the more flask-like shape of the females. Another ecdysis takes place, and within the remains of the larval cuticles the male elongates, coiling on itself until it has attained the full size and form of the adult male [Fig. 2 (3)]. A very thin fourth cuticle is then shed, and the male is ready to burst through the sheath formed of the cast larval skins and begin its wandering in the soil. By this time, owing to its increase in size, the male is generally lying on the surface of the host root, still attached by the anterior end of the sheath but readily dislodged, and just visible to the naked eye [Fig. 3 (1)].

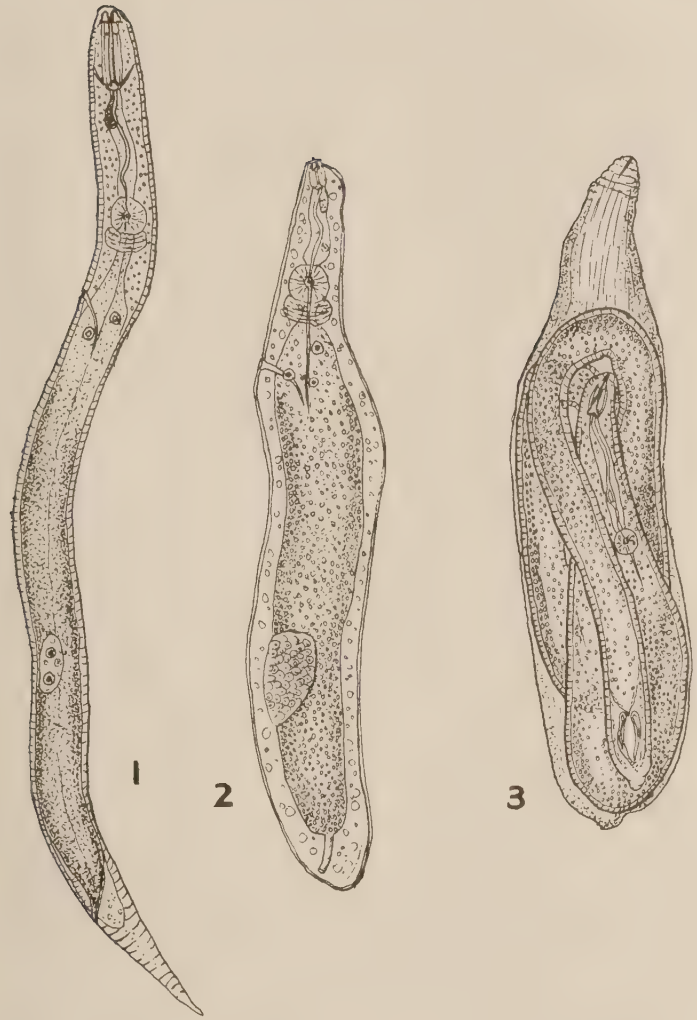


FIG. 2.—*Heterodera schachtii*. (1) Larva. (2) Developing larva. (3) Male coiled within larval cuticle. (All after Strubell.)

The female swells considerably but does not increase much in length, and probably also undergoes third and fourth moults. It bursts through the root cortex, but its head and neck remain embedded in the root and it continues to feed for some time [Fig. 3 (2)].

Posteriorly the vulva is prominent and knob-like. On the body the sub-crystalline coating can be seen ; this may be formed at least in part from the remains of the cast larval cuticles. At this time, while the female is still white, a small quantity of gelatinous substance is exuded from the vulva. According to Sengbusch (1927), this is closely related to fertilization and may serve to attract the male : he found a male *Heterodera* within the drop of jelly on the female on several occasions. Within twenty-four hours the male had left the female, which was then found to contain sperm. It seems probable that the males are polygamous, as they are known to be able to live for two or three weeks in the soil and would thus have the opportunity to fertilize several females. After fertilization the eggs become embryonated in two or three weeks.

The whole development, from the entry of the larva to the production of eggs, takes four to eight weeks, depending on the temperature and probably on the species of host. According to Sengbusch, the female feeds in the roots for about twice as long as the male, and the increase in weight from larva to mature cyst containing up to 400 eggs may be fifty to five hundred times, as compared with ten to fifteen times in the male. The female must therefore require five to thirty times as much nourishment as the male. In cases where the host roots are severely damaged by secondary infections or other unfavourable circumstances, the females may fail to develop or do so very slowly. Sengbusch made a number of counts of males and females developed in both sugar-beet and rape seedlings, and found that for every hundred females there were eighty to ninety males. He found that this relationship remained constant when the manurial content of the soil in which the seedlings were raised was altered, although Molz (1920) claimed to have proved that the sex-ratio of *H. schachtii* is dependent on the manuring of the soil as well as on the species of the host and the temperature.

When the female dies, having completed her function of producing eggs, the cuticle turns brown and tough and forms the resistant cyst which protects the contained eggs, and which under normal soil conditions may last for at least ten years. Chatin (1887)

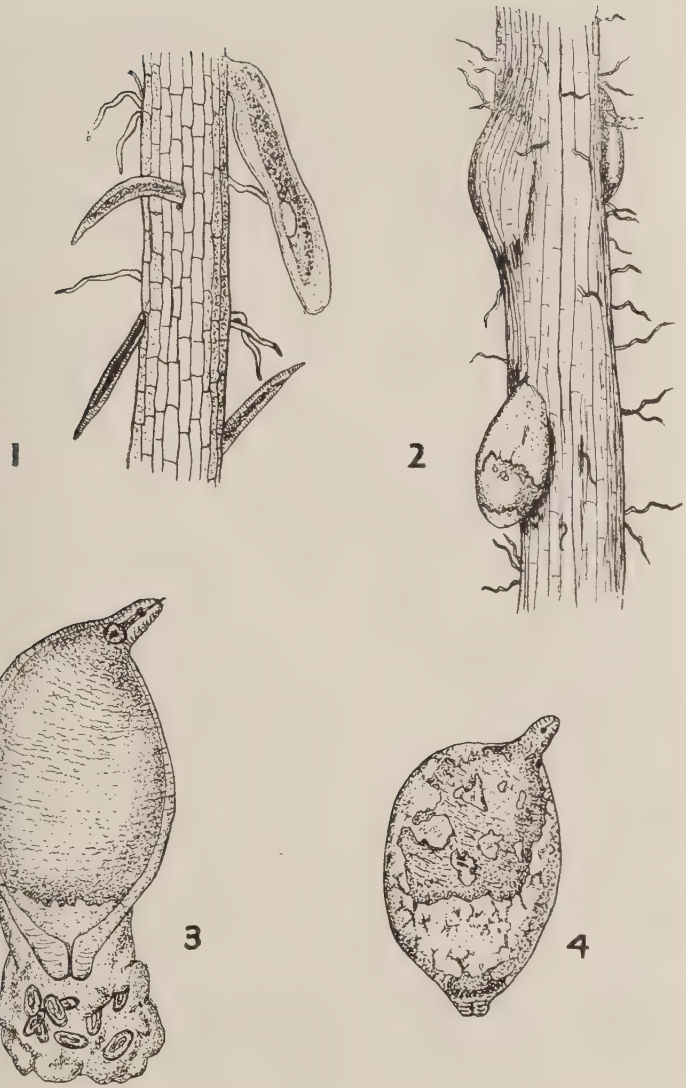


FIG 3.—*H. schachtii*. (1) Root of sugar-beet with developing larvæ and male (above). (2) Females protruding from host root. (3) Mature cyst with egg-sac containing several eggs. (4) Older cyst with sub-crystalline layer. (All after Strubell.)

described the change from the white to the brown cyst as being brought about by the secretion by epidermal glands of mineral and organic substances which form an agglutinated mass, changing the epidermis into the thick, brown resistant cyst wall. He considered that only the females which matured late in the season became cysts in this way, and that the first females to develop were incapable of becoming cysts, their eggs hatching in the season in which they were formed or succumbing during the winter months. It was, however, shown both by Sengbusch (1927) and by Triffitt (1930b) that all mature females are capable of assuming the resistant brown cystic form, and that normally this change takes place within a week or two of fertilization.

Within the protecting cyst the larvae may remain dormant in the soil for several years. Thorne (1923) examined cysts from infested fields which had not grown sugar-beet for periods up to twelve years, and came to the conclusion that by the end of six years most of the larvae had hatched. On the other hand, Jones (1945) considers that at least ten years must elapse before the eelworm population of a completely " beet-sick " field falls low enough for a crop of sugar-beet to be grown with success. This probably depends to some extent on what crops are grown in the meantime. As has already been mentioned, the hatching of the larvae has been shown (Baunacke, 1922a ; Rensch, 1924 ; Nebel, 1926a) to be greatly stimulated by water which has been in contact with the growing roots of certain plants, particularly those which serve as hosts of the eelworm. In the field, hatching also seems to be encouraged by the presence of some plants which do not act as hosts : such plants have been called " enemy plants " (Goffart, 1932b). Certain chemicals such as chloride of lime, when added to the soil, also stimulate the larvae to hatch (Molz, 1930).

Although many of the larvae remain dormant in the cysts for several years, at least some are capable of hatching as soon as they are fully developed. It is therefore possible for a second generation of nematodes to develop in one season. This probably occurs to a very small extent, but there is certainly no likelihood of a third generation as was at one time thought to be the case.

Goffart (1935a) showed that if rape or turnip rape were sown at the beginning of August in infested soil, cysts containing eggs were present on the roots by the beginning of October. If the rape was sown at the beginning of September, cysts were present on the roots

FIG. 4.—Typical patch of " beet sickness " in a crop of sugar-beet. (By courtesy of School of Agriculture, Cambridge.)

FIG. 5. Root of sugar-beet showing "whiskered" appearance and white eelworm cysts. (By courtesy of School of Agriculture, Cambridge.)

by mid-November. The development of the cysts depends on the temperature : if this is below 10° C. cysts may not develop on rape before the spring (Goffart, 1943a). If the nematodes do not complete their development before the winter, they can resume it in the following spring when the warmer weather returns. A fresh invasion of the roots may take place in the spring, so that the same plants may bear two generations of parasites within a year. Autumn-sown mustard is also attacked by the eelworm. Goffart (1942) states that spring-sown rape and mustard probably only support one generation of eelworms a year, and that they bear fewer cysts than sugar-beet. No appreciable damage is caused either to winter or to quick-growing summer cruciferous crops. Hellinga (1946a) held that rape-seed (koolzaad) could bear two generations of sugar-beet eelworms in a season.

Effect on Host

The effects on the aerial parts of the plant of the invasion of the roots by eelworm larvae are chiefly seen in the generally stunted and sickly appearance and resulting poor yield. The leaves are smaller and paler than usual, and there is a marked tendency for them to wilt in warm or sunny weather. In a field of sugar-beet which is infested with eelworm, the infestation usually occurs in patches, and these patches are readily picked out in the growing crop by the sickly appearance of the plants (Fig. 4).

Although no symptoms particularly characteristic of eelworm infection are shown in the aerial parts of the host plants, the invaded roots have a very typical bushy appearance. This is due to the excessive development of lateral rootlets, which give the tap root a distinctly " whiskered " look. They are sometimes termed " hunger roots", as they are produced as a result of the undernourishment caused by the activities of the eelworm larvae in the feeding roots of the plant. New roots are formed to take the place of those which have been invaded, and these themselves are in turn attacked so that even more new ones have to be produced, and a very much branched root system results. When the plants are six to eight weeks old the white females and ensheathed males can be seen on the " hunger roots", and some also appear on the main tap root (Fig. 5). Meanwhile more larvae enter the rootlets from the soil, so that worms in all stages of development may be present at the same time in the roots of a single plant, and the host never has a

chance to grow away from the parasite and develop a healthy root system. The yield from a crop of sugar-beet or mangolds thus attacked is much reduced, and the land on which they have grown is said to be " beet-sick". An example is quoted by Triffitt (1929c) of a field which had previously produced yields of forty tons per acre of mangolds, but gave only fifteen tons when it had become badly infested with eelworm through the repeated growing of mangolds in alternate years for a long time. In the case of sugar-beet, both the total yield of roots and tops and also the sugar content are reduced. This has been shown by several workers who have weighed the tops and roots and analysed the mineral matter of sugar-beets from infested and uninfested soils (Vañha, 1893; Vañha & Stoklasa, 1896; Girard, 1887b; Krüger, Wimmer & Lüdecke, 1935; Hellinga, 1942). Lüdecke (1938) studied the uptake of nitrogen, phosphorus, potassium, sodium, calcium and magnesium by sugar-beet, in infested and uninfested soils, and in soil receiving varying dressings of fertilizer. As a result of analyses of roots and tops he found that in the roots the uptake of nitrogen, potassium and phosphorus was reduced by the presence of nematodes, but that the relationship in the tops was much more complex. He also found that the yield of dried root was always lower in infected plants, except in nitrogen-deficient plots. In the latter there was less reduction in weight of the dried tops, and the sugar content followed the same course as the weight of dry matter. Hellinga (1942) obtained results showing a correlation between the numbers of eelworms in the soil and the mineral status of sugar-beet growing in it: nematode-diseased beet seemed to contain less potassium and more lime and sodium than healthy plants. He also found a negative correlation between the eelworm count of the soil and the yield of sugar-beet.

The anatomy of the roots of the host plants is considerably altered by the presence of *Heterodera* larvae and adults. It was studied by Němec (1911, 1933), who found that syncytia are formed in the secondary cortex and between the vascular tissues of the root by the breaking down of some of the radial walls between the cells. Němec did not see nuclear division in the syncytia, but saw that they contained several nuclei, due to the fact that they are derived from a number of cells, each of which contributes its own nucleus. The walls of the syncytia are much thickened, especially where they border on the vascular bundles, and where they are in contact with

the head of the parasite. In the sugar-beet root itself Němec found that round the syncytium some of the parenchymatous cortical cells divided and formed a small-celled tissue of the nature of a sieve-bundle, but without the sieve-like perforations in the cross-walls. They are apparently not for conduction, as they usually run tangentially to the syncytia. These bundles are not formed in the side roots where most of the nematodes live, but only in the tap root.

Various attempts have been made to correlate the degree of *H. schachtii* infestation of a field with the symptoms shown by a crop grown there. In order to estimate the infectivity of a soil, the eelworm cysts are removed from a sample of the soil by floating them out in water, and the number of infective larvae per unit mass or volume of soil is estimated when the cysts have been opened and the contents examined (for methods, see page 99). By this means the infectivity of various soils can be compared. It is found, however, that the disease symptoms in a crop are not always directly related to the infectivity of the soil, as factors such as soil fertility and climate have a considerable effect on the crop. A fair yield may be obtained on land having an eelworm population which, on other land or in another season, would cause the crop to be a complete failure. In the Fen soil of England experience has shown that if the population of viable eelworm eggs rises above about ten per gramme of air-dried soil, it is unsafe to grow sugar-beet (Jones, 1945).

To some extent the crop can be boosted by suitable manurial treatments, but there comes a time when this is no longer effective and the land is so " beet-sick " that it is unprofitable to grow sugar-beet or mangolds unless it has been given a rest from such crops for several years.

Hosts

The early records of hosts of the sugar-beet nematode are sometimes inaccurate as all cyst-forming *Heterodera* were thought to belong to one species, so that all recorded infections were considered to be cases of sugar-beet eelworm. Biological strains were thought to occur, having their own specialized host ranges, but potentially capable of infecting plants outside their normal range. In the United States the first recognized case of infection with *H. schachtii* was on sugar-beet in 1906 (Shaw, 1915, p. 25), and in 1907 Bessey

found it there on sugar-beet in several scattered localities (Bessey, 1911). In England the first recorded damage was on mangolds in 1928 (Triffitt, 1929c). A light infection had been noticed on beetroot in 1919 (Triffitt, 1931c), and earlier occurrences on other crops had been attributed to the sugar-beet nematode. The parasite was first recorded on sugar-beet in England by Petherbridge in 1934. Long lists of hosts were published by German workers, including some plants now known not to be attacked by *H. schachtii*, but by other species of *Heterodera*. It is however certain that several members of the family Chenopodiaceae, to which sugar-beet belongs, are attacked, and also a number of crucifers such as turnips, rape, cauliflower and mustard. A number of weeds have been found bearing nematodes resembling *H. schachtii*, but it is probable that at least in some cases these belong to other species of *Heterodera* (Goffart, 1936c,d). According to the recent observations of Jones & Petherbridge (1947), Jones (1945), and to a private communication from Jones, the plants listed on p. 25 do probably serve as hosts of the sugar-beet eelworm (see also Jones, 1950[1]).

In addition, *Cheiranthus cheiri* and *Malcolmia maritima* are probably hosts (writer's observation). Hellinga (1941c) states that *Poa annua* can be a host of the sugar-beet eelworm and he also (1942) shows that *Phaseolus vulgaris* may be attacked by this species. He describes the infection of sugar-beet grown in sterilized soil to which cysts from bean roots were added. *Phaseolus vulgaris* and rhubarb are reported also by Hartsuijker (1947) to serve as hosts of *H. schachtii*. Greis (1941a,b) worked on the host range of the sugar-beet eelworm and states that white lupine is attacked by it. In southern France carnation is yet another host of *H. schachtii* (Chatin, 1891d; Pussard, 1946; Nigon, 1947), and Menzel (1941) says that this nematode is known as a pest in vine-growing.

A factor which makes it difficult to be quite certain of the host range of the sugar-beet eelworm is that a similar *Heterodera* (known as *H. schachtii* var. *trifolii* -see p. 32) is often present in soils, attacking clovers, docks and hemp nettle, but differing from the true sugar-beet nematode in that it can only produce cysts on sugar-beet with difficulty. It is as yet uncertain whether or not this should be considered as an unspecialized form of *H. schachtii*,

[1]Jones, F. G. W., 1950.—"Observations on the beet eelworm and other cyst-forming species of *Heterodera*." *Ann. appl. Biol.*, **37** (3), 407-440.

from which the latter has arisen and become so specialized that it can now live only on certain members of the Chenopodiaceae and Cruciferae (and possibly on *Phaseolus vulgaris*). The only sure fact is that the sugar-beet eelworm is now practically confined to members of these two families. The chief importance in knowing the limits of the host range is in relation to the control of the disease caused by the parasite.

CULTIVATED PLANTS

CHENOPODIACEAE

Beta vulgaris—sugar-beet, beetroot, mangold
Spinacea oleracea—spinach
Chenopodium bonus-henricus—Good King Henry or mercury

CRUCIFERAE

Brassica rapa—turnip
B. napobrassica—swede
B. oleracea—cabbage, kale, broccoli, Brussels sprouts, cauliflower
B. napus—rape
B. alba—mustard
B. nigra—black mustard
Lepidium sativum—cress
Raphanus sativus—radish

POLYGONACEAE

Rheum rhaponticum—rhubarb

CARYOPHYLLACEAE

Saponaria officinalis—soapwort
S. vaccaria
Dianthus sp.

AMARANTACEAE

Amarantus quitensis—love-lies-bleeding

AIZOACEAE

Tetragonia expansa—New Zealand spinach

ONAGRACEAE

Lopezia coronata

WEEDS

CHENOPODIACEAE

Chenopodium album—goosefoot, fat hen
C. polyspermum — many-seeded goosefoot
C. rubrum—red goosefoot
C. hybridum—sowbane
Atriplex patula—common orache
**A. confertifolia*—shadscale

CRUCIFERAE

Brassica sinapis—charlock
Capsella bursa-pastoris—shepherd's purse
Erysimum cheiranthoides — treacle mustard
Thlaspi arvense—pennycress
Sisymbrium officinale—hedge mustard
Coronopus ruellii—swine cress
Cochlearia armoracia—horseradish
Raphanus raphanistrum — wild radish

POLYGONACEAE

Rumex crispus—curled dock
R. obtusifolius—broad dock
Polygonum persicaria—persicaria

CARYOPHYLLACEAE

Stellaria media—chickweed

LABIATAE

Galeopsis speciosa—hemp nettle
G. pyrenaica

* Recorded by Thorne (1935a)

Control

Although for over seventy years attempts have been made to eradicate *H. schachtii* from the soil of fields required for the cultivation of sugar-beet or mangolds, no practicable means of doing so have yet been developed. When land was first found to be " beet-sick " and the part played by the nematode was not fully appreciated, the symptoms were thought to be due to a deficiency of some mineral nutrient required by the plants, and various chemical fertilizers were applied. In some cases there was an improvement for one or two years, but this was not maintained. When it was discovered that the trouble was caused at least in part by a parasitic nematode, new methods were tried, which can be roughly classified as chemical and biological. Chemicals have been used for two different purposes in combating eelworm, with the object of killing the nematodes in the cysts in the soil, or with the object of stimulating the larvae to hatch from the cysts ; in the latter case the larvae may then be starved by withholding suitable host plants, or killed by chemical means. The biological methods of control are concerned with crop rotation and the growing of resistant or " enemy " plants.

Chemical Methods.—A great many different chemicals have been tested as agents for killing sugar-beet nematodes, and while some have been effective in the laboratory, their use on a field scale has almost always proved impracticable either on account of the difficulty of applying them efficiently to the soil, or of the excessive cost.

Korab & Butovski (1932) and Korab (1939) found beneficial effects resulting from the application of chloropicrin at the rate of 400 litres per hectare to land heavily infested with the sugar-beet eelworm, and hoped that the chemical could be produced economically for this purpose. The same chemical was found to be an effective disinfectant in field tests made by Decoux & Roland (1938), who also improved yields by applying increased amounts of nitrogenous and potash fertilizers. Van Schreven (1939) in Holland, and Goffart (1939) in Germany tested chloropicrin against sugar-beet nematode, but the chemical has never become widely used in the field.

The most comprehensive work on chemicals for use in the destruction of *H. schachtii* has been recorded by Rademacher & Schmidt (1933). These workers list 321 substances which have been tested in the laboratory against eelworm : thirty-five of them were

also tested in pot experiments, and fourteen in the field over several years. About five substances were considered to be worth further test, namely wood and lignite distillates, condensates of the coal-tar distillation process, " Schnakensaprol " and chloride of lime. But even when used in conjunction with other methods of control, it is considered that these chemicals could hardly be expected to do more than keep the eelworm disease in check. Thorne (1939) drew attention to the importance of a consideration of the soil type if chemicals are to be applied for killing eelworms. He found that about 95 per cent. of the population of *Heterodera* was killed by the application of 800 lb. per acre of calcium cyanamide ploughed in at a depth of 10–12 in., the ground then being harrowed. In the top 2 in. of soil 5 per cent. of the cysts survived on account of the escape of the cyanide gas at the soil surface, while few eelworms below 14 in. were harmed as the chemical did not penetrate so deeply into the particular soil on which the experiments were being conducted. In this field a significant proportion of the nematode population occurred at a depth of between 14 in. and 24 in. Another chemical which proved effective experimentally in controlling sugar-beet eelworm is β-naphthol (McBeth, 1937), but the cost of the chemical alone, if applied at sufficient strength to kill the eelworm, would be many times the monetary value of the land.

More recently Thorne & Jensen (1947a,b) and Fletcher (1947) have tested D-D mixture (two parts of 1,3-dichloropropylene and one part of 1,2-dichloropropane), Dowfume W15 (15 per cent. ethylene dibromide), chloropicrin, propylene dichloride, benzene hexachloride and a mixture of 80 per cent. by weight ethylene dichloride with 20 per cent. propylene dichloride in field tests against the sugar-beet nematode. D-D mixture seemed to be the most promising, but in all cases the sugar-beet became infected, and there was often a considerable production of new cysts.

Since no suitable chemical could be found, which was lethal to the encysted sugar-beet nematode larvae when used on a field scale, some workers tried to discover substances which would activate the larvae and cause them to emerge from the cyst, in which state they would be more easily exterminated either by chemical means or by starvation. Molz (1930, 1932) used chloride of lime in combination with suitable cultivations and crop sequence, while Rademacher (1930) and Rademacher & Schmidt (1933) tested many chemicals in the laboratory in attempts to find one which would cause sufficient

stimulation to be of use on a field scale. No satisfactory system of control by these means was developed, probably because the necessary expenditure in material and labour was greater than the return warranted. At best the resulting improvement was only temporary.

Biological Methods.—As the development of beet sickness was in all cases associated with the continuous cropping of the same ground with sugar-beet or mangolds, the first and most obvious means of fighting it was by a change of crop. It was soon evident that two or three years was insufficient time to allow between the cultivation of crops susceptible to attack, as even if the crops then grown did not suffer much damage, they enabled the nematode to increase in numbers. Hellinga (1941 to 1946) studied the influence of various crops, such as rape, beets, mustard and onions, on the eelworm content of infested soil, and has shown how cruciferous crops increase the infectivity to a marked degree.

Crops such as cereals, legumes and potatoes do not usually serve as hosts, and can be safely grown, though Hellinga (1943a) maintained that *Phaseolus vulgaris* does act as host to the sugar-beet eelworm. Goffart (1933b) recommends winter barley followed by a leguminous crop ploughed in as beneficial to " beet-sick " land. He also says that a four-year crop of lucerne will eliminate the nematode in the absence of susceptible weeds. Thorne (1932) found that the best results with sugar-beet on infested land were obtained when a crop of lucerne was followed by legumes or potatoes. The reasons for the improvement are not very clear, but it is assumed that certain plants such as lucerne stimulate the larvae to hatch from the cysts but are not suitable as hosts, so that the hatched larvae die out and the total eelworm population is reduced, i.e. they are " enemy plants " (Goffart, 1932b).

It is important that weeds which can serve as hosts for the sugar-beet eelworm should be eliminated as far as possible from infested land, as their presence will to some extent nullify the good which may be done by the cultivation of immune crops. The weeds which are particularly dangerous are members of the Cruciferae such as *Capsella bursa-pastoris*, brassicas, *Sisymbrium* and *Sinapis*, chenopods such as *Chenopodium album* and *C. polyspermum*, also *Atriplex*, *Stellaria*, *Rumex*, *Polygonum* and *Galeopsis*. Immune crops which permit the adequate control of weeds are therefore preferable

to those in which such weeds have an opportunity to thrive. Petherbridge, Stapley & Thomas (1938) advise the omission of susceptible crops from " beet-sick " land for five years, and from lightly infested land for three years.

Attempts have been made to develop a variety of sugar-beet resistant to nematode attack. Owen, Thorne & McBeth (1938) were unable, after ten years' work, to find any marked resistance in any of the varieties which they bred and tested.

When large numbers of sugar-beet eelworm cysts are examined, a few are almost always found in which the contents have been destroyed either by fungi or by bacteria, or sometimes by predaceous nematodes. Dollfus (1946) reviews the published work on the parasitism of *H. schachtii* at all stages by fungi and by other nematodes. He cites Goffart (1932a), who found cysts parasitized by *Cylindrocarpon radicicola,* and who also refers to work published by Korab (1929) : the latter described *Torula heteroderae* n.sp., which he had frequently found in eggs and larvae of *H. schachtii* which had been destroyed and had taken on a characteristic reddish-brown colour. Nearly fifty years earlier Kühn (1881, p. 136) had found sugar-beet eelworm cysts parasitized by *Tarichium auxiliare,* while Rademacher & Schmidt (1933) considered that the principal fungal parasite in the cysts was *Isaria destructor,* and more recently Jones (1945, p. 379) found four types of fungal fruiting bodies in sugar-beet eelworm cysts. One type seemed to turn the eggs black ; the others, of which one was a member of the Chytridiales, may have been saprophagous. Roszypal (1934) also found in cysts in Moravia a saprophagous fungus, *Trichosporium populneum,* which appeared to have destroyed eggs and larvae.

Thorne (1925, 1927, 1928a) describes nematodes which feed on *Heterodera.* He found *Mononchus sigmaturus* and *M. papillatus* feeding on eggs, males and immature females, while *Cephalobus oxyuroides* and *Acrobeles büitschlii* were found inside cysts, but he considers that the latter probably feed on the remains of the internal organs of the female, not on the eelworm eggs and larvae. He found no evidence that any of the nematodes in the many cysts which he examined were destroying an appreciable number of *Heterodera* larvae.

It is probable that some of the eelworm larvae, when they have left the cysts and are making their way towards the host roots, succumb to the attacks of predaceous nematodes and nematode-

trapping fungi. The improvement recorded in the crops grown on infested land after the ploughing-in of green manure may be due in part to the encouragement of such predaceous nematodes and fungi by the presence of additional organic matter in the soil. The numbers of nematodes killed in this way, however, are insufficient to make any but a somewhat transitory reduction in the total population. It is interesting to know that in Holland the flooding of land infested with sugar-beet eelworm by sea water for several months completely failed to exterminate the nematode (Murre, 1947).

Trap-Cropping.—Another method of reducing the eelworm population in an infested field is by means of trap-crops. A host plant, such as rape or mustard, is sown and allowed to grow for a week or two in order that the roots shall be as heavily infected with eelworm larvae as possible. Before the nematodes reach maturity the crop is ploughed up and the roots destroyed with their parasites. The method was first devised and tested by Kühn between 1881 and 1891. He sowed summer rape between the rows of germinating sugar-beet. Just before the females in the roots of the rape were ready to produce eggs, the rape was uprooted and left exposed to the sun and wind so that the roots were dried up and killed. The procedure had to be repeated five or six times during the growth of the sugar-beets, and if the weather was not dry and sunny when it was necessary to uproot the trap-crop, the roots had to be collected and destroyed by mixing them with fresh lime. Spiegler (1895, 1907) also used this method with slight differences, and got average increases in yield of sugar-beets of 7 and 3.6 tons per acre, but in spite of this he considered that the procedure was too costly and also rather dangerous, since an unskilled observer or unfavourable weather conditions might delay the lifting of the rape, so that the parasites had time to mature and increase the infestation of the ground instead of decreasing it. More recent work on trap-cropping is described by Greis (1941b) and by Hellinga (1943b). The latter, in small-scale experiments, obtained a considerable decrease in the number of eelworms in the soil after a succession of five trap-crops, but even then did not completely eliminate the parasite.

Legislative Action.—An attempt has been made to prevent the increase and spread of sugar-beet eelworm in England and Wales by legislative measures. The Sugar Beet Eelworm Order, 1943,

schedules certain areas in which sugar-beet eelworm is known to occur, and in these areas prohibits the growing (except under licence) of the host crops (beets, mangolds, spinach and cruciferous crops) on land in which the eelworm is known to exist and on land on which any of these crops has been grown in the preceding two years. In addition to this, no potatoes grown on land where sugar-beet eelworm is known to exist may be moved (except under licence) from off the infested land for planting, except on the same holding. These rules apply to all land, except allotments and private gardens, in the scheduled area, which includes parts of Huntingdon, Suffolk West, Northampton, Cambridge, Norfolk, Lincoln, the Isle of Ely, and the Soke of Peterborough. The order is fully explained by Jones & Petherbridge (1947).

In Canada also, strict regulations have been made with the object of preventing the spread of sugar-beet eelworm (Baker & Thompson, 1943).

Distribution

The sugar-beet nematode is the most widely distributed of the cyst-forming *Heterodera* spp. It occurs in the U.S.A., Canada and Australia, and in the U.S.S.R. (Korab & Butovski, 1939). It is now common throughout Europe, including Sweden, Denmark, Holland, Belgium, France and Germany, and in the countries to the east (Goffart, 1943c). England is probably the most recently affected country, and surveys have been made to determine the exact distribution in the sugar-beet growing areas; Jones & Petherbridge (1947) give maps showing the infested areas.

CHAPTER III

VARIETIES AND RACES OF *HETERODERA SCHACHTII*

Two varieties of the sugar-beet eelworm have been recognized and named *H. schachtii* var. *trifolii* (Goffart, 1932a) and *H. schachtii* var. *galeopsidis* (Goffart, 1936c).

HETERODERA SCHACHTII VAR. *TRIFOLII* GOFFART, 1932

When investigating the oat root nematode, Goffart (1932a) found a strain of *Heterodera* parasitizing red clover, *Trifolium pratense*. As this plant belongs to the same family as peas and beans, he thought the nematode might be *H. göttingiana*, described by Liebscher (1892) from garden peas. Having measured the eggs, larvae and cysts, and decided that they differed from the oat root nematode, he compared his measurements with those given by Liebscher for *H. göttingiana*, and concluded that his strain differed from this species too. In order to distinguish this clover nematode from the other known races of *Heterodera*, he gave it the varietal name of *trifolii*. Later (1944), when he had studied it further, Goffart designated the clover root eelworm as *H. schachtii trifolii*, considering it to be a distinct biological form.

Trifolium repens and *T. incarnatum* were reported to be infected with *H. schachtii* by Hollrung (1890a,b), and a detailed account of an infection—probably of var. *trifolii*—on *T. repens* was given by McBeth (1938).

Morphology

The cysts are typically lemon-shaped, distinctly more elongated than those of *H. göttingiana*, and of a dark brown colour. They have a well developed sub-crystalline layer, and differ from the true sugar-beet nematode in having a distinctly yellow phase when

changing from white to brown. Franklin (1939a) gives the length of the cysts of two populations as 560μ and 540μ, the breadth as 380μ and 360μ, and the length to breadth ratio as 1.5 to 1. The cysts measured by Goffart (1944) were 634μ long and 399μ broad with a length to breadth ratio of 1.7 to 1, but his length measurement includes the neck, while Franklin's excludes it. A small gelatinous egg-sac is usually attached to the cyst and a few eggs are embedded in it. These measured 111μ × 42μ and 98μ × 40μ in the two populations examined by Franklin, while Goffart found them to be 119μ long in one population and 113μ × 45μ in another, and McBeth (1938) gives 114μ × 49μ. The larvae and males resemble those of the sugar-beet nematode. The length of the larvae was 491μ and 504μ in the populations measured by Franklin, 490μ in that measured by McBeth and 481μ and 514μ in Goffart's populations ; the stylet is given as 25–27μ by Goffart and 24μ by Franklin. The males measured 0.63–0.98 mm., according to McBeth, but Franklin's specimens were considerably bigger, averaging 1.32 mm. The copulatory spicules are similar to those in the sugar-beet nematode ; the number of annulations on the head is four or five, as in *H. schachtii.*

Bionomics and Effect on Host

According to Goffart (1944) cyst formation on clover begins in July, and two generations may be produced in the year. No distinct disease of clovers due to this eelworm has been recorded, although heavy infections have been observed in pot-grown plants. McBeth says that the clover roots become somewhat swollen and even galled, the effect resembling that produced by root-knot nematodes. Giant cells are formed in the roots in the presence of invading larvae, disrupting the vascular system and causing the death of the affected rootlet. New rootlets are produced and are in turn attacked, but McBeth never found that the plants were killed. Goffart (1944) also had no certain indication of damage to infected clover plants.

Hosts

Experiments on the host range of the clover root eelworm have been carried out by Goffart (1944) and by Franklin (1945). Franklin found that docks became infected as readily as clovers when grown with cysts removed from the roots of clover : both *Rumex crispus*

and *R. nemorosa* showed this, and cysts from clovers and from docks gave similar results when tested with various other plants. Mangolds and sugar-beet became very sparsely infected : in several experiments no cysts were found, but in isolated cases one or two did occur, most of them very small, transparent and empty. When green peas were tested negative results were at first obtained, but later a few cysts were found on the roots. Some of these cysts were tested with growing clover seedlings and an infection was set up : it was thus proved that cysts of *H. schachtii* var. *trifolii* will infect peas to a limited extent, and the generation on peas was shown to be able to return to clover. Among crucifers tested, neither cabbage nor radish showed infection after eleven months and three months respectively, and only one very small transparent cyst was found on one of four mustard plants after four months' growth with clover cysts. Negative results were obtained in tests of parsley, oats, carrot, forget-me-not, lucerne, French bean and crimson clover (*Trifolium incarnatum*). In Goffart's tests, on the other hand, crimson clover became lightly infected, as also did *Phascolus vulgaris*, *Vicia villosa* and *V. narbonensis*, while peas were not infected. The results of these observations by Goffart (1944) and Franklin (1945) on members of the Leguminoseae are summarized below.

Leguminoseae Infected by Clover *Heterodera*

	Goffart	Franklin
Trifolium repens	++	++
T. pratense	++	++
T. incarnatum	+	—
Phaseolus vulgaris	++	—
Pisum sativum	—	+
Vicia sativa		++
V. villosa	++	
V. narbonensis	+	
Lupinus sp.	—	
Medicago sativa		—

Other plants found by the writer to be infected by *H. schachtii* var. *trifolii* are *Stellaria media, Galeopsis speciosa, Rumex* spp., *Isatis tinctoria, Brassica alba* (very lightly) and *Beta vulgaris* (lightly).

Specific Status

The morphology of the male, the shape of the cysts, and the presence of the sub-crystalline layer, together with the host range, all indicate that the clover root eelworm is not identical with *H. göttingiana*, the pea eelworm. The yellow phase in the develop-

ment of the cysts and the host range distinguish it from the sugar-beet eelworm. No other differences have been described, and it is best regarded at present as a variety, and referred to as *H. schachtii* var. *trifolii*.

HETERODERA SCHACHTII VAR. *GALEOPSIDIS* GOFFART, 1936

Morphology

Goffart (1936c) described a variety of *Heterodera* found in Germany parasitizing the roots of the common hemp nettle, *Galeopsis tetrahit* L. The cysts were 0.727 mm. long (including the neck, which averaged 0.058 mm.), and 0.504 mm. broad, giving a ratio of length (excluding neck) to breadth of 1.327 to 1. The cysts contained variable numbers of eggs, which resembled in form those of the oat root nematode, averaging $108\mu \times 44.5\mu$. The larvae were 485μ long, and the mouth stylet was 22μ, the same length as the greatest body width. There were no morphological differences between this race and the sugar-beet eelworm.

Hosts

Goffart was able to remove 75–100 cysts from the roots of hemp nettle, and these he added to a pot of sterilized soil in which he grew oats, sugar-beet, potatoes, red dead nettle (*Lamium purpureum*) and hemp nettle. Each species was tested twice, but only the hemp nettle became infected. Goffart concluded that this eelworm differed from the three well known heteroderas attacking oats, sugar-beet and potatoes, and should be regarded as a variety of the sugar-beet eelworm which had become specially adapted to *Galeopsis*, hence he named it *H. schachtii* var. *galeopsidis*.

Since 1936 *Galeopsis* has been recorded as a host of *H. schachtii* by Petherbridge & Jones (1944) and by Jones (1945). In the former instance lemon-shaped cysts were found on the roots of *G. speciosa* (which is very nearly related to *G. tetrahit* and sometimes considered a variety of it) growing amongst sugar-beets which were not infected, though in another part of the same field they were infected. In other fields, hemp nettle was attacked where no sugar-beet eelworm was found. In the case reported by Jones, *G. speciosa* was found infected on a farm where sugar-beet eelworm was present, but the cysts on the hemp nettle were smaller than the normal ones occurring on sugar-beet. Jones (private communication) states that

the following plants are attacked by the *Galeopsis* eelworm : *G. speciosa*, *G. tetrahit*, *G. pyrenaica*, *Stellaria media* (cysts common), *Saponaria vaccaria*, *S. officinalis*, *Veronica agrestis* (cysts common), *Rumex* sp. (cysts uncommon), red clover (cysts uncommon), French and runner beans (only small cysts), *Beta vulgaris* red beet, mangold—and *Spinacea glabra* (in the last two species only eight cysts were found on 200–250 plants). In this race the cysts have a definite yellow phase, like that in the clover eelworm and the potato root eelworm. It will be noticed that most of the hosts have also been recorded as hosts of *H. schachtii* var. *trifolii*. In the opinion of Jones, and also of the writer, there is a strong likelihood that the two varieties are identical. It is difficult to be certain of this until more is known of the host range of the population studied by Goffart (also Jones, 1950—see footnote p. 24).

RACES OF *HETERODERA SCHACHTII*

Other populations of eelworms which may prove to be varieties of *H. schachtii*, or even specifically different from the latter, have been found from time to time. Triffitt (1929d) describes nematodes of the genus *Heterodera* infecting sea maram grass (*Psamma arenaria*) found in Devonshire. This plant has since been found bearing eelworm cysts at Southport in Lancashire, in Scotland and near Dublin. It therefore seems probable that a strain of *Heterodera* parasitizing sea maram grass is fairly widespread. Triffitt was unable to observe differences between this nematode and *H. schachtii* of sufficient importance to necessitate separating it as a distinct species. Its most striking characteristic is that the cysts on the host roots are completely hidden by grains of sand partly embedded in a gelatinous mass [Fig. 6 (4)]. If the sand grains are removed, one, two or sometimes as many as five females will be found embedded in the jelly, and, if they are mature, embryonated eggs and one or more males may also be present [Fig. 6 (3)]. The cysts are lemon-shaped, of a dark brown colour, and on the whole are not unlike those of *H. schachtii*. Triffitt made measurements of the different stages of the parasite, but the material at her disposal was all preserved, and she considered that the cysts were not fully mature. One difference noted by her was that the postanal region was longer in males from maram grass. The spicules, also, apparently differ somewhat in shape from those of *H. schachtii*, the tip being

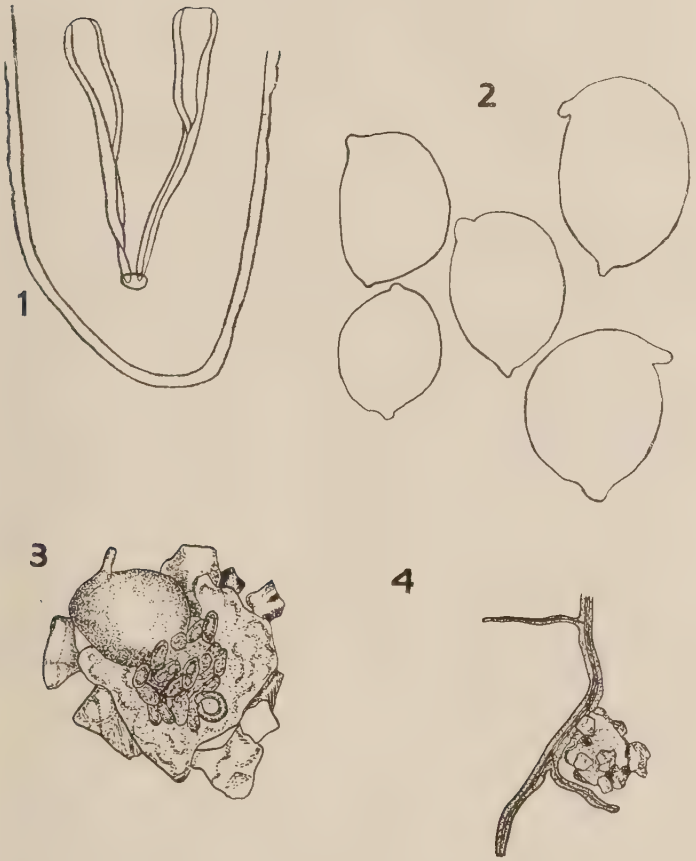


FIG. 6.—*Heterodera* from sea maram grass (*Ammophila arundinacea*). (1) Male tail showing spicules. × about 1300. (2) Cysts. × 25. (3) Cyst removed from root showing egg-sac and sand grains. × 50. (4) Rootlet bearing cyst covered with sand grains. × 20. (Nos. 3 and 4 after Triffitt.)

rolled rather than bidentate (Franklin, 1940c) Fig. 6 (1). Further observations on this race of *Heterodera* are, however, required before it will be possible finally to determine its identity.

Another undetermined form of *Heterodera* has been found attacking cultivated *Myosotis* (Franklin, 1940a). In this race the cysts are smallish and lemon-shaped. In an experiment, *Myosotis sylvatica* grown in soil with them became heavily infected, and clovers (*Trifolium pratense* and *T. repens*) also showed a slight infection in one instance. However, as the soil used had not been sterilized, the clover root eelworm may also have been present. In other tests, *Myosotis* did not become infected when grown with cysts of *H. schachtii* removed from mangold roots. Larvae of the *Myosotis* root eelworm average 479μ in length, which is not very different from the length of *H. schachtii* and *H. gottingiana* larvae. The cysts are approximately 0.68 mm. × 0.51 mm. (length excluding neck), and the ratio of length to breadth is 1.3 to 1.

Steiner (1947) mentions a cyst-forming species of *Heterodera* which apparently only attacks plants of the genus *Polygonum*, occurring in the eastern and central U.S.A. The cysts are characteristically lemon-shaped and occasionally forms occur which might be mistaken for *H. rostochiensis* (Cunningham & Mai, 1947) but for the fact that, instead of the rows of punctations found in that species, the wall has "linear meandrous ornamentations". This race of *Heterodera* was found in sixty-one out of sixty-six roots of knotweed examined in a survey reported by the United States Department of Agriculture (1944). This species has recently been described as *H. weissi* by Steiner (*Proc. Soil Sci. Soc. Fla*, 1949 (Year 1942), **4**B, p. 99).

CHAPTER IV

HETERODERA CACTI FILIPJEV & SCHUURMANS STEKHOVEN, 1941

In 1932 Adam described in detail a strain of *Heterodera* which had been found parasitizing cactus plants at Maartensdyk, in Holland. He received for examination three plants of *Phyllocactus akkermannii* and one of *Cereus speciosa*, all showing marked symptoms of disease attributable to the nematodes, which were very numerous on the roots and collar of the plants. All stages except young females were present, and Adam gives detailed measurements of the larvae, males, eggs and cysts. He was unable to investigate the host range of this race, but sent some material to Goffart who (1936c) published the results of hatching tests carried out on the cysts.

Morphology

The cysts are small, just under 0.5 mm. in length and very nearly spherical, but have a definite prominent vulva, giving them a lemon-like shape [Fig. 7 (1)]. The small (young) ones are golden yellow and the bigger ones dark reddish-brown ; the cuticle is annulated and there are no punctations and no sub-crystalline layer. Adam makes no mention of an egg-sac, which is presumably absent. The mean length (excluding neck) of 100 cysts from *Phyllocactus* was 445μ, the neck 52μ, and the breadth 447μ. The ratio of length to breadth was 1.045 to 1. Fifty cysts from *Cereus* gave mean measurements of 431μ $\times$ 424μ, neck 44μ, with a length to breadth ratio of 1.014 to 1. The eggs were slightly reniform, and measured 114μ $\times$ 43μ, and 110μ $\times$ 46μ respectively from the two hosts, giving length to breadth ratios of 2.62 to 1 and 2.36 to 1 respectively.

The larvae resemble those of the sugar-beet eelworm morphologically, and are approximately the same length. Only fifteen were

measured from *Phyllocactus* and eleven from *Cereus*, and they averaged 485.8μ and 473.6μ respectively.

Six males were examined: they had an average length of 1.01 mm., and the tail was short and bluntly rounded as in the sugar-beet eelworm. The spicules also resembled those of the latter, ending in a blunt, bidentate tip, and being 33.5μ long [Fig. 7 (2 and 3)].

Bionomics

Adam gives no information about the bionomics of the *Heterodera* from cacti. The specimens which he describes were received in May and June, and at that time apparently there were present on the roots some females, a few males, and brown cysts containing embryonated eggs. The cactus plants had probably been grown in a greenhouse.

Goffart (1936c) tested some cysts from cactus plants during the month of May to determine whether the larvae would hatch in response to stimulation by root diffusates of oat, sugar-beet, potato and cactus. He immersed ten batches of cysts in distilled water, and every second day counted the larvae which emerged until, by the tenth day, the numbers had fallen off. He then replaced the water by root diffusates of oat, sugar-beet, potato and cactus in duplicate batches. On the twelfth, fourteenth and sixteenth days he again counted the hatched larvae and found that the cactus root diffusate had caused some stimulation and the sugar-beet root diffusate a slight stimulation, as compared with the distilled water controls, but oat and potato root diffusates had had no effect. From the figures he gives, the proportion of the hatched larvae which emerged after stimulation with the various root diffusates can be calculated as under :—

Stimulant	Hatched 1st–10th days (in distilled water)		Hatched 12th–16th days (after stimulation)		% Hatch after stimulation	
	a	b	a	b	a	b
Water (control)	1,212	623	37	37	2.96	5.61
Potato diffusate	588	541	19	31	3.13	5.4
Oat ,,	98	58	10	6	9.26	9.38
Beet ,,	194	334	39	103	16.7	23.6
Cactus ,,	510	386	343	299	40.2	43.7

In another experiment there was no indication of the stimulation of larvae in sugar-beet cysts by cactus root diffusate.

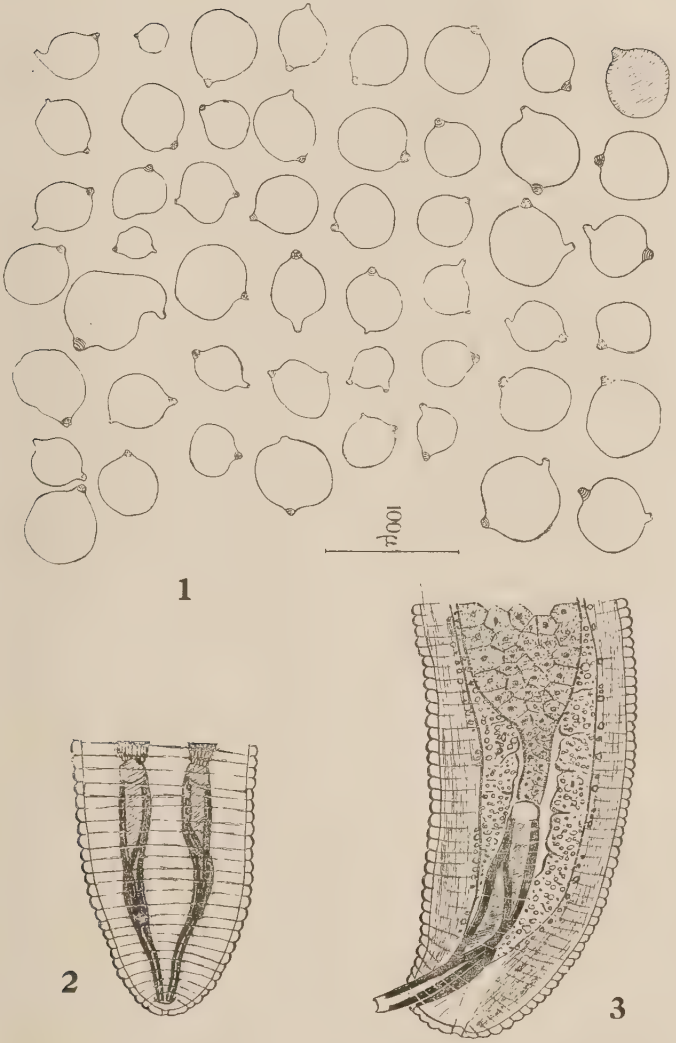


FIG. 7.—*Heterodera cacti*. (1) Cysts. (2) Male tail, ventral aspect. × 1120 (3) Male tail, lateral aspect. × 1120. (All from Adam.)

From these results Goffart concludes that the cysts from cacti are *Heterodera schachtii* and that, though they have become somewhat adapted to cacti, they have not altogether lost their power of responding to stimulation by sugar-beet root diffusates. He did not carry out infection tests owing to lack of material.

Hosts

Only *Phyllocactus akkermannii* and *Cereus speciosa* are known.

Specific Status

From Adam's morphological descriptions and Goffart's work on the hatching of the larvae, Filipjev & Schuurmans Stekhoven (1941) considered this strain of *Heterodera* to be a distinct species, and named it *H. cacti*. In the writer's opinion this decision is justified, in spite of Goffart's hatching tests, on account of the distinctive features shown by the cysts, namely their small size, their almost spherical shape, the absence of sub-crystalline layer and egg-sac, and the golden-yellow phase of the young cysts. Apart from the size, these features are also present in cysts of *H. rostochiensis*, but the latter differ in having no prominent vulva and in possessing regularly arranged punctations on the cyst wall. *H. cacti* also differs from *H. rostochiensis* in that its larvae do not hatch to any marked extent in response to potato root diffusates.

CHAPTER V

HETERODERA MAJOR (O. SCHMIDT, 1930)

OAT ROOT EELWORM, WHEAT ROOT EELWORM (AUSTRALIA), CEREALS ROOT EELWORM

Syn. *H. schachtii* A. Schm. subsp. *major* O. Schm., 1930
H. schachtii var. *avenae* (Mortensen, Rostrup & Kølpin Ravn, 1908)
H. avenae Filipjev, 1934

Nomenclature

The cereals root eelworm has been known in Europe since the end of the nineteenth century as a parasite causing disease and loss to crops of oats and, to a lesser extent, of wheat, barley and rye. In South Australia on the other hand, where it was first noticed in 1906 and since the 1920's has given trouble in several districts, it occurs chiefly on wheat although it also attacks other cereals. In 1933 it was discovered, for the first time on the American continent, in Ontario (Putnam & Chapman, 1935), and by 1945 (Baker, 1945a) it was known to be widely distributed in southern Ontario, but had not been observed anywhere else in the Western Hemisphere. There, as in Europe, oats are the usual host, and considerable damage may be caused, but Chapman (1938) describes severe damage to winter wheat in spring, following a mild winter.

The first records of *Heterodera* on cereals in Britain were those of Theobald (1908a, 1909a) on oats in Lincolnshire and on wheat in Kent respectively. In 1933 a severe attack on oats was recorded from a field near Shrewsbury, and in the following year in Cheshire (Edwards, 1935). Since then it has been observed in many parts of England and Wales, and in Scotland (Cameron, 1946), but not in Eire (Carroll, 1939).

It was referred to in Germany as *H. schachtii* by Kühn (1874) and Hollrung (1892a onwards). In 1892 Voigt thought that sugar-beet and cereals were attacked by two different strains of the sugar-beet nematode, each having a definite preference for its own host

plants and not readily parasitizing any other species. Hansen (1897) in Denmark also described the eelworm from oats and came to a similar conclusion. The eelworm of cereals thus came to be known as the "oat nematode", and in the Danish records of plant diseases it had become so familiar by 1908 that it was referred to (Mortensen, Rostrup & Kølpin Ravn, 1908) as *H. schachtii* var. *avenae*, although no description of it was ever published under this name. It occurred in Holland, Norway and Sweden and, particularly in the last-named country, it was already of sufficient importance by the beginning of the twentieth century for a considerable amount of research to have been directed towards finding methods of reducing the damage done by it.

In 1930, O. Schmidt thoroughly investigated the question of the differences between sugar-beet and oat nematodes, and concluded that the latter should be termed a subspecies, which he formally described as *H. schachtii* subsp. *major*. This subspecies was raised to specific rank by Franklin (1940c) under the name *H. major*, since no formal description or designation had accompanied the earlier publication of the varietal name *avenae* in the Danish literature. Filipjev (1934) adopted the specific name *avenae* for this eelworm, but this name is invalidated by Schmidt's earlier (1930) use of *major*.

Morphology

Male.—Few descriptions have been published of males of *H. major*. Triffitt (1929c) gives the average length as 1.36 mm., and the writer found the mean length of one hundred worms to be 1.38 mm. Triffitt found the ratio of length to breadth to be 39 to 1, and the stylet to be 28μ and the spicules 36μ in length. The males thus differ little in dimensions from those of the sugar-beet nematode, though possibly they are very slightly smaller. The head has five annulations anterior to the shallow constriction separating it from the rest of the body.

The distinctive character is the shape of the spicules (Fig. 8 (1)): these are of the same curved form as those of *H. schachtii*, but the posterior part is slender and rolled so that the distal limb appears to be in the form of a narrow tube. In the length and shape of the tail and in the cuticular markings, the male of *H. major* is similar to that of the sugar-beet nematode.

Female.—The young females and cysts are of the typical lemon shape, comparatively large and coated with a thick white subcrystalline layer which, when chipped off the mature cyst, reveals a tough, dark brown, almost black protective wall beneath. The cyst measurements published by various workers vary considerably. Goffart (1930a) gives the mean length as 536μ, breadth 419μ, neck 52μ and ratio of length (excluding neck) to breadth as 1.155 to 1. In 1932 (a) he measured two populations and gives the mean lengths as 713.6μ and 741.8μ, breadths 505.8μ and 515.5μ, and necks 76.9μ and 68.9μ respectively. The ratios of body length to breadth were 1.25 to 1 and 1.39 to 1. Triffitt (1929c) found the cyst to average 710μ $\times$ 500μ, and Franklin (1940c) gives the ratio of body length to breadth as 1.44 to 1.

The cyst wall has punctations arranged irregularly [Fig. 14 (1)]. A small gelatinous egg-sac is produced, but eggs are not usually found in it. There is no yellow phase as the maturing cyst changes from white to dark brown.

Eggs.—The eggs, of which there may be over 200 in a fairly large cyst, are rather longer than those of the sugar-beet nematode. Putnam & Chapman (1935) give the size as 115μ $\times$ 49μ; Goffart gives 118μ; Triffitt, 106μ $\times$ 41μ. The ratio of length to breadth is thus in the first case 2.35 to 1, and in the last 2.59 to 1. Millikan (1938b) found the eggs of a population from wheat in South Australia to be approximately 126μ $\times$ 28.5μ, giving a ratio of 4.4 to 1, which is very much greater than the values found by other workers. It appears possible that there is a mistake in the value of 28.5μ given for the breadth of the egg.

Larvae.—The greater length of the larvae of this species is the reason for the specific name *major*. O. Schmidt (1930) was the first to make large numbers of measurements of the larvae, and to realize that they are distinctly longer than those of the sugar-beet eelworm. He gives the length as 575μ, as compared with 470μ for the sugar-beet nematode. The writer, using the standard technique for making these measurements as described by Fenwick & Franklin (1942) finds that the length varies between 567μ and 576μ in four different populations, with a mean of 575μ. Goffart (1930a) gives 560μ, Putnam & Chapman (1935) 530-550μ, while Triffitt (1929c) gives 470μ and Millikan 430–490μ. It is curious that, while the eggs measured by Millikan were somewhat larger than those measured by any other author, his larvae are considerably

smaller than any except those measured by Triffitt. Most authors agree, however, that the larvae of *H. major* are between 540μ and 580μ long, hence the name *major* is justified, at least as applied to the larval stage of the nematode.

Before it was generally recognized that the oat root eelworm is specifically different from the sugar-beet eelworm, a great deal of work was done in measuring the length of the larvae of the two races. Schmidt (1930) first adopted the idea of measuring large numbers of larvae of several populations of oat and sugar-beet eelworms, and he was able to show conclusively that those from oats were always, on the average, significantly longer than those from sugar-beet. He also found, when measuring larvae of the oat eelworm mechanically removed from cysts, that a proportion of them were distinctly shorter than the rest, being approximately the same size as the sugar-beet larvae, about one-fifth of all the larvae from a cyst being of the small type. He considered that these smaller larvae would not have hatched spontaneously, and appeared to be malformed; Schmidt referred to them as *minor* forms. Goffart (1932a) also made a great many measurements of larvae of this species, and in all cases found that in each cyst the larvae were of two types, long and short, the smaller being between 440μ and 530μ, the others 530–638μ [Fig. 9 (1)]. Most of the large ones, but only some of the smaller ones, were capable of hatching spontaneously. The small (*minor*) ones seemed to hatch in response to repeated stimulation by root diffusates of rape, but not of oats: a few were capable of penetrating the roots of sugar-beets. The proportion of *major* to *minor* larvae varied. The significance of the presence of these small larvae is unknown, in view of the established specificity of the oat nematode. It is probable that at least some of them are larvae injured in the process of extracting them from the cysts. It is rather easy to rupture the larval cuticle and, when this happens, some of the contents immediately burst out of the larva, and it contracts. It is not always obvious when this has occurred, but it certainly appears to have happened to the larvae illustrated by Schmidt

FIG. 8.—(1) *Heterodera major*. Male tail showing spicules with rolled tips. × about 1300. (2) *H. gottingiana*. Male tail showing three-toothed spicules × about 1300. (3) *H. humuli*. Male tail with spicules and gubernaculum. (4) *H. humuli*. Cysts with gelatinous egg-sacs. (From F. G. W. Jones). (5) *H. cruciferae*. Cyst with egg-sac and embryonated eggs: patches of sub-crystalline layer on cyst wall. (6) *H. cruciferae*. Male tail showing spicules and gubernaculum.

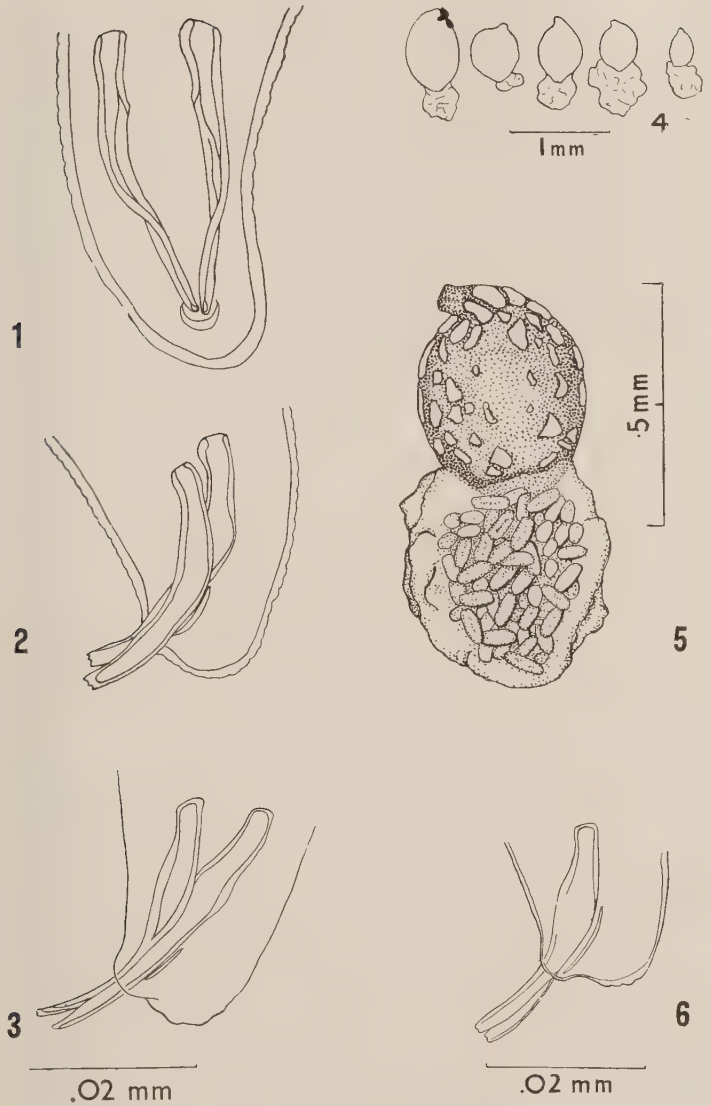


FIG. 8.

(1930) and this is supported by his referring (p. 431) to most of the *minor* larvae as " . . . Larven, die einen verkümmerten Eindruck machten. Während gesunde Larven eine ziemlich feste und widerstandsfähige Cuticula besitzen, waren diese ' Kümmerlinge ' oft geplatzt oder sie könnten sich nicht in normaler Weise strecken, sondern lagen zerknickt und zerknickert unterm Mikroskop. Meist waren auch die innern Organe schlecht oder gar nicht ausgebildet." [. . . larvae which gave the impression of being stunted. While healthy larvae possess an apparently firm and resistant cuticle, these ' weaklings ' were often burst, or they could not extend in a normal way, but lay bent and crumbled under the microscope. Most of them also had the internal organs badly or not at all developed .

Apart from the length, the larvae resemble those of *H. schachtii*. Goffart measured the stylet and found that it was 26μ long ; Triffitt gives its length as 22μ, and Millikan 24.8–29.2μ.

Bionomics

If the roots of fortnight-old oat seedlings from soil infected with *H. major* are examined, in either autumn- or spring-sown crops, it will be found that larvae have entered near the growing point and have established themselves close to the central vascular cylinder. In cereals sown out of doors in autumn, the larvae invade the roots and begin to develop during the early part of the winter, but adults are not found until the following summer. Goffart (1939c) showed that if oats are grown during the winter in infested soil in the greenhouse, the larval development is not arrested, and he found cysts on the roots in January, five months earlier than would occur normally out of doors. These cysts were only two-thirds as big as normal ones. He mixed 700 of them with sterilized soil ; in the following September only 65 of these cysts could be recovered, and of these only seven contained healthy larvae. Only very few larvae entered the roots of oats sown with these cysts. In another interesting experiment Goffart grew oats in the greenhouse during the winter with new cysts which had all been formed during the previous summer. Although he found larvae already in the oat roots in October, no cysts developed until the following June, in contrast to the result when the plants were grown in soil containing older cysts. He concluded that larvae from newly formed cysts require nine months to mature, while those from older cysts are able, under

greenhouse conditions, to mature five months earlier than they would do naturally.

Schmidt (1931) found out, as a result of experiments in which he made frequent sowings of oats in infested soil, and examined plants at intervals over a period of fifteen months, that the larvae invade the roots in the greatest numbers from March to May [Fig 9 (2)]. In June the numbers fall off very markedly, and from July until December very few enter the roots. Goffart's work agrees with these results. Schmidt (1931) also performed experiments showing that in the laboratory larvae were apparently not stimulated to hatch in the presence of the root diffusates of oats or wheat, or of bone oil. In another experiment, he sowed oats at weekly intervals throughout the year in pots of infested soil which were examined after a fortnight's growth in the greenhouse : the roots contained the greatest numbers of larvae in the spring and early summer, although the tests were always carried out at approximately the same temperature and soil moisture content. At the end of May, in another hatching experiment, he tested twenty-four oat nematode cysts separately in root diffusates of sugar-beet, rape, oats and potatoes, and found that four cysts out of the twenty-four, in diffusates from rape (one cyst), potato (one cyst) and oats (two cysts), became emptied of all but unhealthy-looking larvae. The other twenty cysts, though full of larvae, were unaffected by being soaked in the diffusates.

Although, according to Schmidt's work, oat root diffusates apparently do not stimulate oat nematode larvae to hatch, Putnam & Chapman (1935) showed that the larvae travelled at least eight inches towards oat roots from a point where no plants were growing. While their direction of travel may have been due to chance, it seems likely that it was influenced by the growing oat plants.

Thus, the oat nematode differs from the sugar-beet nematode firstly in that the principal attack on the host plants is restricted to the period from March to June, at the time of greatest vegetative activity of the host plants, while sugar-beet nematode larvae can attack at any time, given young host plants and suitable conditions of temperature and moisture. Secondly, the host plant apparently plays no part in stimulating the hatching of oat nematode larvae, while it has been shown that the larvae of the sugar-beet nematode are stimulated to hatch by the presence of root diffusates of their host plants. Thirdly, it has been shown that even in the green-

house, where larvae from newly formed cysts may enter the roots of oat seedlings in the autumn, no second generation is produced before the following summer. In contrast to this, with sugar-beet nematodes it is possible for two generations to develop in one year, given favourable conditions. Schmidt points out that several features of the life-history of *H. major* still remain unexplained. The precise factors governing the hatching of larvae are not known : for example, it cannot be explained why all the larvae in a cyst do not hatch in the same year—it is evident that they do not, since in infested soil many cysts contain a greater or less proportion of unhatched eggs (apparently healthy) amongst the empty egg membranes. As the larvae do not seem to need the presence of growing host plants to activate them, Schmidt asks what happens to larvae which hatch when there is no host available. How long are they able to survive in the soil without feeding, until cereals are again growing ? Goffart says that they can live free in the soil for about six months.

Having hatched and found a suitable host, the oat nematode larvae enter the roots close to the growing point and, according to Putnam & Chapman (1935) and Goffart (1939c), they orientate themselves lengthwise, almost always with the head towards the growing point, and close to the vascular cylinder. Goffart (1941a) found the majority of larvae in the lower parts of the root system. The development of the larvae has not been studied in very great detail, but is probably closely similar to that of *H. schachtii*. Under Canadian conditions (Putnam & Chapman, 1935), in spring-sown oats the worms have become flask-shaped at the end of four weeks, and the sexes can be distinguished. In another week mature males and females may be found, and at six weeks some of the latter may contain eggs. About nine weeks after the oats have been sown, some of the cysts on the roots will probably be found to have turned brown beneath the thick, white sub-crystalline layer, and the first embryonated eggs may be present in another two or three weeks. Putnam & Chapman found hatched larvae inside newly formed cysts four months after the host plants on which they had developed had been sown.

In Australia, where the cereals root eelworm prefers wheat to oats, Millikan (1938b) observed that development was more rapid in wheat than in other cereals. In the roots of susceptible varieties of oats, the larvae took six weeks to develop to the slightly swollen

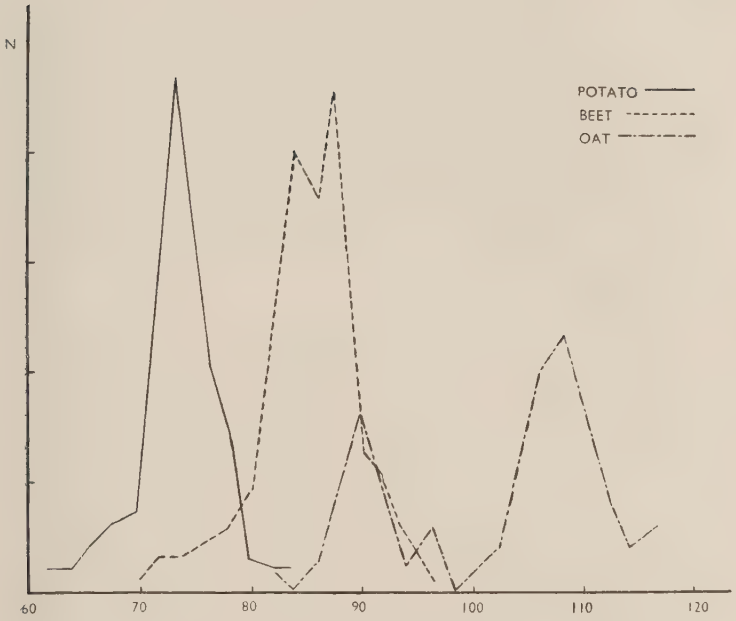


Fig. 9 (1)

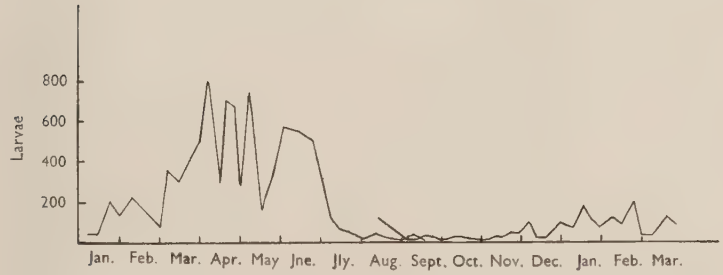


Fig. 9 (2)

Fig 9.—(1) Graph of lengths of larvae of potato, oat and beet eelworms. N = number of larvae. L = length in units of t = 5.5μ. (After Goffart 1934.) (2) Graph showing rate of hatching of larvae of *Heterodera major* throughout the year. (After Schmidt 1931.)

stage, while in resistant varieties there was no apparent development of the entered larvae, even after sixteen weeks.

As soon as they are ripe the cysts very easily become detached from the host roots, which by this time are somewhat tough and wiry, and cysts are often difficult to find if plants are dug up for examination. In this respect this species differs from *H. schachtii*, whose cysts remain comparatively firmly attached to the roots of the host plant. The sub-crystalline layer, which is such a marked feature of the young cyst while it is still attached to the root, is very soon lost when the cyst becomes loose in the soil.

Effect on Host

A full account of the disease as it affects oats in Canada is given by Putnam & Chapman (1935), while Garrett (1934) and Millikan (1938a,b) describe the symptoms shown by wheat in South Australia. Usually the first hint of the presence of root eelworm in a cereal crop is the appearance of patches of weak, stunted plants. In Canada, about two weeks after the plants have appeared above ground, the affected ones seem to stop developing and take on a "staring" appearance, the leaves standing stiffly erect, with the edges rolled inwards slightly. Later, the oldest leaf turns a characteristic brick red, the colour starting at the tip of the leaf and working downwards. Sometimes the same effect is also seen in the second leaf. This coloration varies somewhat according to the mineral status of the soil: it lasts for seven to ten days, and then fresh leaves are produced, and the discoloured ones die off and disappear. The plants never fully recover, and their further development depends on soil and weather conditions. In Australia, root-rotting fungi are nearly always associated with eelworm infestation. The above-ground signs of disease vary from "no-growth" patches in a field, to crops which are merely slightly stunted and of a yellowish-green colour; in other cases, the aerial parts of heavily infected plants may look quite normal. Goffart (1941a) compared the size and development of leaves and ears in attacked and healthy plants, and found considerable reduction in the attacked plants.

The invaded roots are characteristically deformed. They are much shorter than normal, and where a worm is developing there is always a swelling, with numerous side roots. If the side roots are also invaded, they too remain short and become swollen, and in their turn produce side roots. The whole root system thus becomes

abnormally branched and curtailed. This condition, as shown in extreme cases, has aptly been called " coral root ".

The entry of the larvae into the host root has not been studied, but is probably achieved in the same way as by *H. schachtii*. As in sugar-beet roots, giant cells soon appear near the head of the parasite, causing obstruction of the conducting tissues, and in a short while several side roots begin to develop nearby. One of the effects of the very much reduced root system is that the parasitized plant is much more sensitive to dry conditions in the superficial layers of the soil than is the normal plant. During a dry spell, therefore, infected plants suffer more than healthy ones and may die out altogether. But Goffart (1941a) considers that unusually high rainfall in April and May increases the injury due to nematodes.

Hosts

The host range of *H. major* is practically confined to graminaceous plants. The following have been reported as attacked by the oat nematode, the presence of other species of *Heterodera* being unlikely in all cases except those indicated :—

(A, B, C, G) *Avena sativa* (oats)
(A, B, C, G) *A. fatua* (wild oats)
(A) *A. sterilis*
(C, G) *Bromus secalinus* (chess)
(G) *B. mollis*
(A) *B. rubens*
(A, B) *B. sterilis*
*(C) *Chenopodium album*
(G) *Festuca pratensis*
(A, B, C, G) *Hordeum vulgare* (barley)
(A, C, G) *H. distichum*
(A) *H. murinum*
(A) *Lolium hybridum*
(A) *L. italicum* (Italian ryegrass)
(B) *L. perenne* (perennial ryegrass)
(G) *L. westerwoldicum*
(A) *Phalaris canariensis*
(G) *P. paradoxa*
(G) *P. arundinacea*
*(A) *Pisum arvense*
(A, B, G) *Secale cereale* (rye)
*(A) *Sonchus asper*
*(A) *Trifolium resupinatum*
*(G) *T. pratense*
(A, B, C, G) *Triticum vulgare* (wheat)
(C) *T. spelta* (speltz)
(A) *T. durum*

A = Australian record
B = British record
C = Canadian record
G = German record

* Some of these records may be due to the presence of a second race of *Heterodera* in the soil.

It is very curious that in all parts of Europe and in Canada, oats is the principal host of the cereals root eelworm, with wheat and barley also attacked, sometimes quite severely, and rye only slightly affected, while in Australia wheat is the most severely attacked, with oats and barley suffering less damage and rye again

only lightly affected. There is, so far as is known, no reason to think that the Australian eelworm is a different species from that occurring on cereals in Europe and Canada, but it may be regarded as a race which differs biologically in preferring wheat to oats. Maize was carefully observed by Goffart (1941a), but he could find no infection in it.

Resistant Varieties

It was noticed by the earlier European investigators that certain varieties of barley were less severely affected by the oat root eelworm than were others. Nilsson-Ehle (1920), Jörgensen & Thomsen (1928) and Wålstedt (1929) all found that in infested land certain varieties of barley bore far fewer cysts than others. Nilsson-Ehle found that Chevalier varieties of barley showed resistance which was inherited in cross-breeding according to Mendelian laws. The Danish workers (Jörgensen & Thomsen) found that the barley Abed Rex was resistant as compared with other varieties tested.

Millikan (1938b) in Australia tested 200 varieties of wheat, oats and barley during two years in an attempt to find evidence of resistance to the eelworm. He found that different varieties of all three cereals showed varying degrees of resistance as judged by the different numbers of cysts on the roots and their relative rate of development. Resistance was shown to a greater extent in oats and barley than in wheat, but in no case was complete immunity observed. Of the varieties of wheat tested, the *T. durum* varieties were slightly more resistant than the *T. vulgare* varieties, but only three showed any considerable degree of resistance, namely Indian Runner, Huguenot and Sepoy × Dan W5497 P3-3-2. On the other hand, contrary to the results obtained in Europe, marked differences in resistance were exhibited by certain varieties of oats. There was apparently no correlation with the two species involved, *Avena sativa* and *A. sterilis*, but wild oats, *A. fatua*, and two crosses of this species carried particularly large numbers of cysts. The oat roots were distorted to a less extent than infected wheat roots. Four oat varieties were classed as resistant, namely Gidgee, Guyra, Mortgage Lifter and Mulga, while three others were moderately resistant, namely Algerian Selection P4, Dawn Selection W393U1 and Kareela. Resistance in barley varieties was intermediate between that in oats and wheat, and was not related to the two-row or six-row type. Twelve barley varieties were classed as moderately

resistant : Algeria V, Bay Brewing, Black Hull-less, Chevalier × Pryor, Deputy, Gisborne, Golden Grain, Orge 14J, Pearl, Roseworthy, Oregon × California Feed, Trabut and Tunis. Chevalier was classed as susceptible, and Kniver Chevalier as very susceptible.

Five varieties of Australian oats tested in England in soil heavily infected with *H. major* showed no resistance to infection, namely Mulga, Burke, Gidgee, Guyra and a wild cross.

Nilsson-Ehle (1920) and Goffart in his earlier work (1932a) found no resistant variety of oats, but Goffart continued his testing of oats, and records (1941a) that the varieties Adler and Heines Silber, during four years' testing in the laboratory and field, were less severely attacked and gave higher yields than others tested. Winter oats were less severely affected than spring varieties. Some spring barleys were less damaged than others, but none of the spring wheats tested by Goffart showed any resistance.

Control

As with *H. schachtii*, various attempts have been made to destroy *H. major* in the soil by means of chemicals (Edwards, 1938), but the same difficulties have been encountered, and no satisfactory method has been found. In Australia, some improvement in the health of affected crops resulted from the application of certain chemical fertilizers, particularly zinc sulphate at the rate of 15 or 30 lb. per acre together with 1 cwt. of superphosphate, but there was no reduction in eelworm attack. Goffart (1941b) states that the yield from a diseased crop may be increased by the use of a quick-acting nitrogenous fertilizer, but that the number of cysts in the soil is also much increased.

The only control recommendations which can be made are concerned with crop rotation and methods of cultivation. Cereals, particularly the more susceptible ones, should be spaced as widely apart as possible in the rotation, and susceptible grasses should be avoided. It is uncertain to what extent the cereals eelworm cysts in an infested soil become emptied in the absence of host plants. The results of rotation experiments carried on for four years in Australia on land infested with the wheat strain are given by Millikan (1938b). Although a three years' fallow, or two years under insusceptible crops followed by one year's fallow, resulted in a marked reduction in the number of cysts in the soil, the eelworm did not die out completely. Weeds are probably unimportant as

"interim" hosts between susceptible crops (Goffart, 1941a), so that it should be possible in time to starve out the nematode.

As a cultivation measure, consolidation of the surface soil in order to preserve the moisture is helpful in areas liable to drought. Putnam & Chapman in Canada recommend ridging during the winter to allow frost to penetrate the soil, as they observed that root infestation and disease due to eelworm were more severe in areas which by reason of snowdrifts had had some protection from intense cold during the winter.

Trap-cropping with cereals has not been fully investigated, but might prove useful, though it could probably only be effectively carried out (in the Northern Hemisphere) between March and June, when the eelworm is most active.

The most promising line of approach lies in the development of resistant varieties of cereals. Since some varieties of barley have shown resistance to the European cereals root eelworm, and some varieties of oats have shown resistance to the Australian race, it seems probable that other and perhaps more strongly resistant varieties of either could be bred for use on infested land.

Spread

The spread of *H. major* is most likely to occur on implements and on the feet of man and animals, and occasionally by flooding and wind storms.

Distribution

H. major is widely distributed throughout Europe, having been known for about seventy years in the Schleswig-Holstein district of Germany, and for over fifty years in Sweden and all parts of Denmark; eelworm disease of oats has been reported also in Holland (Dijkema, 1947; Hartsuijker, 1947) and Norway (Schøyen, 1926), and in the British Isles it was first noticed forty years ago (Theobald, 1908a). It is also known in South Australia (Davidson, 1930; Hickinbotham, 1930; Millikan, 1938a,b), and in Ontario, Canada (Putnam & Thorne, 1935), and has been reported from Casablanca, Morocco (private communication). The distribution in relation to the type of soil on which the disease is most prevalent has not been widely studied, but usually disease is most marked where susceptible cereals have recurred frequently in the crop rotation

(Thomas, Brown & Willis, 1946), and on light, somewhat acid soils. In Canada, Putnam & Chapman (1935) studied the correlation between soil type and parasite, and found that 90 per cent. of the infestations were on a silty clay loam, strongly alkaline (pH 8.2–8.3), deficient in available phosphorus, but with a moderate amount of organic matter. The other prevalent soil type in the infested area is a light gravelly loam, with a neutral to alkaline reaction and fairly low in organic matter ; only about 5 per cent. of the infestations, none of them severe, were found on this soil. The results of soil analyses and counts of eelworm cysts in the infested soils of Australia showed no correlation between infestation and soil type.

CHAPTER VI

HETERODERA GÖTTINGIANA LIEBSCHER, 1892

PEA ROOT EELWORM

Syn. *H. schachtii* pea strain.

Liebscher, in 1890, reported that a disease of peas due to the nematode *H. schachtii* was causing severe crop losses at the Agricultural Institute at Göttingen. In 1892 he published a description of the eelworm and of the symptoms in the host plants. A comparison of the parasite with the familiar sugar-beet and oat nematodes led Liebscher to conclude that he was dealing with a different species of *Heterodera*, and he named it *H. göttingiana*.

Capus (1917, 1918) described a disease of peas due to what he took to be *H. schachtii*, but which in all probability was *H. göttingiana*, in the Gironde district of France, and the same trouble has been reported from many places in Britain (Ogilvie & Mulligan, 1931 ; Miles & Miles, 1946) since the first record by Theobald (1912b).

Morphology

Male.—The male of *H. göttingiana* has not been described in detail. Filipjev (1934) gives the length as 1.26 mm., with spicules 44μ and stylet 37μ long. Franklin (1940c) found the mean lengths of males of two populations from peas to be 1.22 mm. and 1.29 mm., twenty-five and fifty-three individuals respectively being measured. Twenty-five males from the roots of broad beans gave an average length of 1.21 mm. According to these measurements, the males of this species are slightly shorter than those of the sugar-beet nematode. The mean length of the spicules of ten males was 32.5μ, and of the stylet 27.5μ, both being smaller than the figures given by Filipjev, but differing little from those for *H. schachtii*.

No morphological differences between males of this species and of *H. schachtii* have been described, except in the form of the tip of the copulatory spicules. These, as shown by Franklin (1940c), are somewhat truncate and end in three minute teeth, instead of two as in the sugar-beet eelworm [Fig. 8 (2)].

The number of annulations on the head is rather difficult to distinguish, sometimes appearing to be five as in *H. schachtii*, sometimes seven or eight, in which case they are narrower than when only five are visible.

Female.—The cysts are typically lemon-shaped, and tend to be round rather than elongated. Franklin (1939a) gives the average cyst size as 0.605 mm. × 0.503 mm., with the neck 0.051 mm., and length (excluding neck) to breadth ratio as 1.203 to 1. The cyst measurements given by Filipjev (1934) are 0.650 mm. × 0.470 mm., the length probably including the neck in this case. Liebscher gives the mean size of cysts from peas as 0.651 mm. × 0.466 mm., from horse beans as 0.578 mm. × 0.417 mm., and from vetch as 0.612 mm. × 0.398 mm., the length probably including the neck in all cases. Goffart (1941f) re-examined the Göttingen population and gives mean cyst measurements of 682.7μ × 490.9μ and ratio of length to breadth 1.39 to 1.

The cyst wall has minute, irregularly arranged punctations, but it differs from the sugar-beet eelworm in its darker colour and in having no sub-crystalline layer. The ripe female turns gradually from white through pale to dark brown with no yellow stage. A gelatinous egg-sac may be found at the vulva of cysts which are

still attached to the host root, and some eggs may be present in this, but it is absent from cysts extracted from soil.

Eggs.—Rather varied figures have been given for the size of the eggs. Liebscher (1892) gives $245\mu \times 108\mu$: this is obviously erroneous, and the figures should probably be divided by two, giving $122.5\mu \times 54\mu$. Filipjev (1934) gives 108μ, while the writer finds the average to be $101.5\mu \times 53.9\mu$, and Goffart (1941f) $110\mu \times 44\mu$. The eggs are definitely rounder and more barrel-shaped, with more convex sides, than those of the sugar-beet and oat nematodes.

Larvae.—The mean length of the larvae as given by Liebscher is 462μ, while Goffart gives 456.2μ, and numerous measurements made by the writer give a mean of 487μ, all figures falling well within the limits of values given for *H. schachtii*. In other details of morphology, too, the larvae of the pea root eelworm resemble those of the sugar-beet eelworm.

Bionomics

It has been stated (Franklin, 1940c) that larvae of *H. göttingiana* show some stimulation by pea roots in the summer, hatching more readily in their presence, but are not influenced in the early spring. No results of hatching experiments have been published except by Goffart (1941c) who found no stimulation by root diffusates of peas, oats, potato or sugar-beet. He concluded that the hatching of the larvae depends principally on the time of the year, taking place chiefly in spring, since peas sown in April bear many cysts by July, those sown in July have only a few cysts on the roots in September, while later-sown peas remain practically free from attack.

Walton, Ogilvie & Mulligan (1934), when growing peas in soil infested with *H. göttingiana* in a cold greenhouse, first found cysts on 22nd April on the roots of plants sown at the end of November, showing that hatching of the larvae must have taken place during the winter or early spring. Peas were sown in the same ground on 19th May, but no infection could be found in the middle of July. The same result was found in peas sown in another infested soil in the following November, while in a repetition of the spring sowing a very light infection was found at the end of June. Peas sown in June were not infected at the end of three weeks. It was thought that the temperature in the greenhouse may have affected the results since in an outdoor experiment repeated sowings of peas

throughout the summer were all infected, though only lightly during July and August. The cysts took about five weeks to develop during the summer, but eight to twelve weeks in the spring.

Capus (1917, 1918) made observations agreeing with these, on peas growing in infested soil out-of-doors in the Gironde Department of France. In this district peas are grown between the rows of vines during winter and spring; they are often grown every year on the same ground, but only in alternate rows, so that each row is planted with peas every second year. Sowings are made from November to January, and Capus first observed infection on the November-sown plants in the second half of May; plants sown in January were only slightly affected. On one occasion, in the month of August, he found dead female *Heterodera* on the pea roots. He also observed that a field which shows a uniformly heavy infestation in the spring may, when peas are sown in it in the following winter, give at first only patches of diseased plants, the patches spreading to cover the whole area during the course of the season. It appears from this and from the finding of dead worms on the roots in August, that numbers of the nematodes die both on their host and in the soil during the hot, dry period of the year. Soil temperatures, according to Capus, may reach 47° C. or even a little higher during the summer, and this temperature might well prove lethal to the parasites.

A very curious phenomenon shown in some cases of pea sickness is the suddenness with which an outbreak appears. As an example may be quoted a case mentioned by Miles & Miles (1946). In 1945 peas were grown for the first time on a field in Wiltshire, where they failed in patches. Eelworm cysts found on the roots were apparently the cause of the failure of the crop. A five-course rotation had been followed on the land during the previous eighteen years, vetches, seeds and hay occurring in three out of every five years. These crops, each having a greater or smaller proportion of leguminous plants, would provide good material for the development of a nematode preferring such hosts. Since it has been found in experiments (Franklin, 1945) that *H. göttingiana* will not to any great extent attack clovers (which would probably be the principal leguminous plant in the seeds and hay mixtures), it may be that this and similar sudden outbreaks are due to the presence of a large population of *H. schachtii* var. *trifolii*, which attacked the peas in

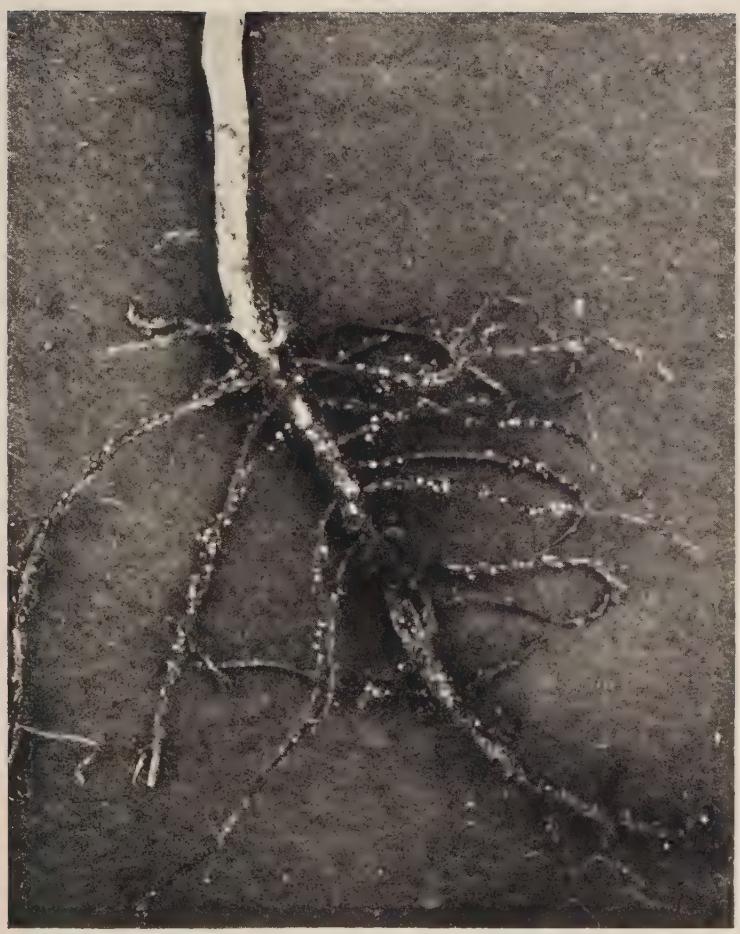


FIG. 10.—Pea root covered with cysts of *Heterodera göttingiana*. Note absence of bacterial nodules. (By courtesy of School of Agriculture, Cambridge.)

FIG. 11.—Bad patch of "sickness" in peas due to *Heterodera göttingiana*. Note difference in height between healthy and diseased peas. (By courtesy of School of Agriculture, Cambridge.)

the absence of any other legume. It has been shown that this variety is capable of reproducing on peas at least to a limited degree. On the other hand, it may be a case of a population of *H. göttingiana* which can thrive on clovers and vetches, and had in fact always done so until the crop of peas was grown. To settle the question a morphological examination of the parasites is needed.

Effect on Host

More work has been done on attempts to control the disease of peas caused by eelworm than on the bionomics of the parasite itself. From the beginning, observers have noticed that the diseased plants are almost always affected by a fungal foot-rot. Liebscher (1892) mentions no fungus, but Capus found that *Fusarium vasinfectum* was almost always present. Walton, Ogilvie & Mulligan (1934) and Triffitt (1931b) also observed a species of *Fusarium*, while Powell (1939) found the rot-producing fungus *Aphanomyces euteiches* Drechsler. Edwards (1935) found the latter or *Thielavia basicola* invariably present, sometimes both together.

The symptoms of pea sickness have been described by Liebscher, Capus, Triffitt, Walton *et al.*, and Powell. The plants are stunted and of a poor colour, with yellow-green leaves, and they die off early in the season. The foot-rot takes the form of a blackening and rotting of the stem tissues at ground level, while the roots are soft, brown and poorly developed, and bacterial nodules are sparse or absent (Fig. 10).

The disease often occurs in more or less circular areas in a field (Fig. 11), though in bad cases the whole area is affected.

Yields from diseased crops are of course much reduced, and Liebscher (1890, 1892) gives figures for crops harvested from some infected plots which were considerably less than the seed sown. In this instance peas had been grown annually on a number of plots receiving various manurial treatments from 1877 onwards : disease became evident in 1884, and grew more severe from year to year. Nematode cysts were first observed on the pea roots in 1890.

The effects of attack by nematodes and foot-rot fungus on different varieties of peas were studied by Walton, Ogilvie & Mulligan (1934). Most varieties were severely affected, and although one or two, notably Dwarf Defiance, grew better than the others, this may have been due to a stronger resistance to the prevailing climatic conditions or to the fungal foot-rot, rather than to the nematode.

Powell (1939) studied the effect on the host of nematodes and fungus (*Aphanomyces euteiches*) both separately and together and concluded that, while each alone may cause disease, *Heterodera* is the primary factor. Capus found an instance of eelworm-infected peas in which no fungal parasite was observed, and came to the conclusion that the fungus enters the pea plant through lesions caused in the first place by the nematodes.

Hosts

Liebscher (1890, 1892) grew a number of plants on the "pea-sick" plots at Göttingen, and found numerous cysts on the roots of the following: *Pisum sativum* (all varieties), *Vicia faba*, *V. sativa*, *V. cordata*, *V. monantha*, *V. hirsuta*, *V. villosa*, *V. serratifolia*, *V. narbonensis*, *Ervum lens*, *Lathyrus cicer*, *Cicer arietinum*; isolated cysts were found on *Lupinus luteus*, *L. cruckshanksii*, *L. albus termis* and *Soja hispida* [= *Glycine hispida*]. Cereals, brassicas and beets grown in the same land were not infected. Goffart (1941f), testing a number of plants on the same ground forty-five years later, found the following additional species of *Vicia* to be infected: *V. amphicarpa*, *V. canadensis*, *V. disperma*, *V. leucospermum*, *V. serotina* and *V. ramonica*. He found no cysts on lentil, lupine or *V. hirsuta*, which Liebscher had found to be infected, nor on *V. cracca*, red clover, white clover, oats, potato or sugar-beet. It is possible that the clover eelworm (*H. schachtii* var. *trifolii*) was formerly present on this land (i.e. in Liebscher's time), since two of the species of *Vicia* (*V. narbonensis* and *V. villosa*) which Liebscher found infected are said by Goffart to be hosts of the clover eelworm. This surmise is supported by the fact that on two or three occasions the writer has grown *Trifolium pratense* and *T. repens* in clean sand with cysts removed from pea roots, but neither clover became infected. The dwarf bean (*Phaseolus vulgaris*) did not become infected by the pea eelworm.

Walton, Ogilvie & Mulligan (1934) found peas, broad beans (*Vicia faba*) and vetches to be infected by *H. göttingiana*, and also found cysts on the roots of red clover, but many common weeds (including *Vicia sepia*) as well as cabbage, kale, potato, oats, sweet pea (*Lathyrus odorata*), beets and mangolds were free from cysts. Possibly in this case also the clover eelworm was present in addition to the pea eelworm.

Specific Status

It was largely the results of Liebscher's (1890) experiments showing the restricted host range of the pea root eelworm, supported by the smaller size of the cysts and the consistent absence of a sub-crystalline layer, that convinced him of the specific status of the nematode which he named *H. göttingiana*. The later work of Goffart (1941f) helps to confirm Liebscher's opinion. The same characters have been observed in the *Heterodera* of peas examined by the writer, and the host range of the population met with in the south-west of England also corresponds in general with that of other populations from peas. These characters, together with the typical form of the spicules, are sufficient to establish the specific status of the pea root eelworm.

Control

Chemical Methods.—Various chemicals have been applied to "pea-sick" soil in attempts to control the disease. Sulphate of ammonia, sulphate of potash and dung (Ogilvie & Mulligan, 1933; Walton, Ogilvie & Mulligan, 1934) were without effect. Formalin and calcium cyanamide (Ogilvie & Mulligan, 1935; Walton, Ogilvie & Brian, 1935; Walton, Ogilvie & Mulligan, 1935) did not appreciably reduce the numbers of eelworms on the roots of peas grown afterwards, though the crop was much improved. The improvement after calcium cyanamide was thought to be due to the increased nitrogen available, and it was concluded that one of the effects of the combined attack on the plants by nematodes and fungi was to disorganize the nitrogen metabolism (see also Ogilvie, Hickman & Walton, 1938). This may be correlated with the fact that bacterial nodules occur infrequently or not at all on the roots of heavily infected plants.

Biological Methods.—No appreciably resistant varieties of peas having been discovered, it is obvious that the only practical means of avoiding pea sickness is by withholding susceptible crops from infested land for several years. As the host range of *H. göttingiana* is so restricted, there should be adequate scope for a wide rotation. Walton found that a three years' rest from peas is insufficient to clear infested land of the eelworm, though the growth of a subsequent crop of peas may be much improved. In districts where

there is a hot dry season, as in the Gironde, soil cultivations calculated to dry out the cysts would probably help to reduce the infestation.

Distribution

Germany, France and Great Britain are the only countries, so far as is known, in which *H. göttingiana* has been reported. The outbreaks of pea sickness described by Capus (1917, 1918) in France are assumed to be due to this species, but without definite confirmation. Dispersal of *H. göttingiana* probably only occurs when infested soil is transported mechanically in the various obvious ways.

UNDETERMINED *HETERODERA* SPP. ON OTHER LEGUMES

Soya beans (*Glycine max*), adzuki beans (*Phaseolus angularis*), kidney beans (*P. vulgaris*) and multiflora or scarlet runner beans (*P. coccineus*) are attacked by a distinct race of *Heterodera* in Japan (Ito, 1921 ; Fujita & Miura, 1934). This race will not attack *Pisum sativum*, *Vicia faba*, *V. sativa*, *Phaseolus limanensis* (Lima bean), *Vigna sinensis* (cowpea), *Arachis hypogaea* (peanut), *Trifolium pratense*, *Lupinus albus*, *Lathyrus tingitanus* (Tangier pea) or cereals, potato, sugar-beet and brassicas. Liebscher (1892) found soya beans lightly infected with *H. göttingiana*, but several other plants which he found to be hosts of the pea eelworm are not apparently infected by the eelworm found in Japan.

According to Ito, the mature cysts are lemon-shaped and become reddish-brown : fragments, apparently of a sub-crystalline layer, are present at first on the body wall, but easily fall off. The female body length (presumably excluding the neck) is 550–710μ, and the breadth 310-523μ. Over 300 eggs measuring 90-111.6μ × 39.6–43.2μ may be present in the cyst, and are said to be expelled from the reproductive aperture, often covered with a sticky substance. The mature worms are said to store larvae in a squirming mass. The larvae measure 414–432μ in length with a mouth spear of 19–25.5μ.

Insufficient information is available to form a definite opinion on the status, specific or varietal, of the eelworm of soya beans, but judging by the host range as recorded by Fujita & Miura, and by the presence of a sub-crystalline layer recorded by Ito, it is not *H. göttingiana*.

Lucerne (*Medicago sativa*) has been reported (Filipjev & Schuurmans Stekhoven, 1941, p. 598) as heavily infected with *Heterodera* in the experimental field at Poltava (Ukraine). The species of eelworm in this case is not certain, but the writer has failed, in pot experiments, to infect lucerne with the clover root eelworm, and Goffart also (private communication) states that *H. schachtii* var. *trifolii* does not attack *Medicago*.

CHAPTER VII

HETERODERA CRUCIFERAE FRANKLIN, 1945

BRASSICA ROOT EELWORM

Since the earliest studies of the sugar-beet eelworm in the 1870's and '80's, it has been known that *H. schachtii* will attack cruciferous plants. Kühn, in 1881, records infections in a number of species of *Brassica*, and many other investigators have found cysts on these plants. The first published suggestion that there might also be a strain or species of *Heterodera* which attacks crucifers, but not sugar-beet or mangolds, is given by Petherbridge & Jones (1944). They found cysts on the roots of swedes and kohlrabi (*Brassica napobrassica* and *B. oleracea gongyloides*) in a field in Norfolk where no infection could be found on sugar-beet growing together with these brassicas. They also observed on allotments near Peterborough that, while red beets were not infected, there were cysts on various brassicas. In 1945 Franklin described a new species of *Heterodera*, *H. cruciferae*, probably the same as that mentioned by Petherbridge & Jones, infecting a number of cruciferous plants, but not chenopods.

Morphology

Male.—The males are a little smaller than those of *H. schachtii*, but no other differences have been observed. Six males from broccoli plants had an average size of 1.2 mm., six from swedes averaged 1.177 mm., and two from cabbage measured 1.21 mm. and 1.13 mm., giving an average for the fourteen of 1.179 mm. Males of

H. schachtii are usually 1.4–1.6 mm. long, with a stylet of 29–30μ. The stylet in the male of *H. cruciferae* is about 25μ. The spicules measure 32μ, and are of the same form as those of *H. schachtii* (Fig. 8 (6) p. 47). The head region, with four or five annular striations, also resembles that of the sugar-beet eelworm.

Female.– The cysts of *H. cruciferae*, while definitely lemon-shaped, are more rounded than those of *H. schachtii* and are also somewhat smaller. The mean measurement (Franklin, 1945) of 100 brassica eelworm cysts from cabbage was 559.8μ × 432.5μ (length excluding neck), giving a length to breadth ratio of 1.29 to 1 as compared with 854.6μ × 574.2μ with a ratio of 1.49 to 1 for 122 *H. schachtii* cysts from mangolds. Eighteen cysts of *H. schachtii* from brassicas averaged 858.3μ × 520.4μ with a length to breadth ratio of 1.65 to 1, showing that cysts of this species remain relatively larger and longer than those of *H. cruciferae*, even when developed on cruciferous plants. In colour and in the presence of minute irregular punctations and a sub-crystalline layer, the brassica eelworm cysts resemble those of the sugar-beet eelworm, but they have a well developed gelatinous egg-sac, which often becomes nearly as big as the cyst itself [Fig. 8 (5)]. Varying numbers of eggs—sometimes as many as 100–200—are embedded in the jelly, and very often one or two males may be present, usually apparently dead. On maturing the cysts change colour from white to brown with no yellow phase.

Eggs.—The eggs are small, 93.5μ × 46.75μ, only twice as long as broad, and therefore rather rounder than the larger eggs of the sugar-beet eelworm.

Larvae.—Large numbers of larvae from radish and cabbage measured by Franklin (1945) averaged 418μ in length, which is significantly smaller than the average for sugar-beet eelworm larvae measured by the same technique and from the same hosts: 360 larvae of the latter species averaging 461μ. No other morphological differences have been observed.

Bionomics

No extensive hatching experiments have been recorded for this species, but there is some indication that the larvae hatch in rather greater numbers in the presence of root diffusates of certain cruciferous plants, namely mustard, cabbage, swede and radish, than in distilled water or in sugar-beet root diffusate. White females have

been found on the roots of brassicas growing out of doors during the winter (December and February), as well as during the summer, so that it seems likely that hatching may occur at any time of the year, and that more than one generation may develop during the year.

Effect on Host

Since brassicas may be attacked by both *H. schachtii* and *H. cruciferae*, which two species have only recently been distinguished, it is impossible to know which species is involved in the older records of eelworm disease of these plants. Instances of disease associated with eelworm cysts on the roots of brussels sprouts, kale, broccoli, cabbage, cauliflower, swede, turnip and other brassicas have been recorded from time to time in the Ministry of Agriculture Monthly Summaries of Plant Pests and Diseases (not published). In some cases the crop has been a complete failure, in others the failure has been patchy. Very often cysts have been found where little damage is in evidence, from which it seems likely that if brassica crops were carefully examined the brassica eelworm would be found to occur much more frequently than is supposed. Brassicas on the whole have a marked ability to produce new roots and, particularly in well established plants, roots attacked by nematodes can quickly be replaced by new ones. In cases of crop failure, fungal parasites have possibly been present in addition to the eelworms.

Hosts

All varieties of *Brassica* which have been tested have become infected, and also a number of other cruciferous plants, but no member of any other family has so far been found to act as host to *H. cruciferae*. Cysts have been found on the following plants :—

Brassica oleracea capitata—cabbage
B. o. botrytis—broccoli, cauliflower
B. o. gemmifera—brussels sprouts
B. o. acephala—kale, curly kale
B. o. gongyloides—kohlrabi
B. napobrassica—swede
B. rapa—turnip
B. napus—rape
Alyssum maritimum—sweet alyssum
Crambe maritima—sea kale
Cheiranthus allionii—Siberian wallflower
Cheiranthus cheiri—wallflower
Iberis umbellata—candytuft
Lepidium sativum—garden cress
Raphanus sativus—radish
Sinapis alba—mustard

Control

No methods of control have been worked out. The eelworm may obviously be spread if infected brassica seedlings are transplanted into fields or gardens, or if any plants grown in infested soil are transplanted with some of the soil. Great care should be taken to keep seed beds free from infection.

Distribution

The only records of *H. cruciferae* are in England and Wales.

CHAPTER VIII

HETERODERA HUMULI FILIPJEV, 1934

In 1895 (a,b) Percival described a disease of hops which he thought was due to *H. schachtii*. He found cysts on the roots of plants showing the " nettlehead " or " skinkly " condition, and came to the conclusion that the parasite was the cause of the disease. Infections by the same nematode were recorded by Theobald (1907, 1908b, 1909b, 1910, 1912a), and in 1925 Duffield investigated hops with the " nettlehead " disease and decided that although cysts of *Heterodera* were present on the roots, they were not the cause of the disease. Ware (1939) considered " nettlehead " to be a virus disease, but Ogilvie (1939) could not confirm this. In 1927 Duffield published a paper dealing with the morphology and biology of the eelworm which he found on the hop roots.

On the evidence of morphological data given by Voigt (1894) for the cysts, and by Triffitt (1929c) for all stages of the eelworm from hops, Filipjev (1934) named this nematode *Heterodera humuli*, considering that it differed specifically from the other known members of the genus.

Morphology

Male.—The males are smaller than those of *H. schachtii*, but according to the measurements of the writer, the mouth stylet is surprisingly big. The mean length of eleven males was 1.032 mm., while the stylets of five worms averaged 31.01μ. Triffitt (1929c) gives measurements of 0.85 mm. and 27μ for length and stylet respectively. She states that the spicules are 32μ, while the writer found them to average 34.6μ in three individuals; accurate measurements are difficult to make, however, since the spicules are curved as in the other species of the genus, and are seldom seen in one plane from

end to end. The tip of the spicule is apparently a simple point, and the terminal limb is slightly twisted (Fig. 8 (3)). The cuticular striations on the head are rather shallow and it is uncertain how many are present, but probably there are four or five as in *H. schachtii*.

Female.— The cysts of *H. humuli* are small and light brown, with a fairly well developed sub-crystalline layer. In shape they are ovoid with a slightly prominent vulva which places them in the lemon-shaped class but is rather easily overlooked. There are minute punctations on the wall, arranged irregularly, and a gelatinous egg-sac is produced in which eggs are not usually found (Fig. 8 (4)). Duffield, who examined a great number of cysts, states (1927) that there are 50-150 eggs in each. His cysts were 0.45–0.75 mm. long, and 0.34 to 0.47 mm. broad, while Triffitt gives the average size as 0.534 × 0.402 mm., with a neck 0.07 mm. long. Voigt's cysts were 0.564 × 0.377 mm. in size. These measurements agree fairly well together, and are considerably smaller than those for the sugar-beet nematode. Another point of difference is in the thickness of the cyst wall, which in this species is thinner and more delicate than in *H. schachtii*.

Eggs.—Triffitt gives 89μ × 42μ as the size of the eggs: Duffield found them to be 92–95μ · 47 48μ, and the writer found them to average 93μ × 37.1μ. The ratio of length to breadth, according to the three workers, is therefore 2.12 to 1, about 2 to 1, and 2.5 to 1 respectively. They are thus about the same size and shape as those of *H. cruciferae*.

Larvae.—These are comparatively small: Duffield gives their length as 380μ, Triffitt as 390μ, and the writer found the average length to be 399.7μ. This is smaller even than those of *H. cruciferae*, which are about 418μ. The stylet is also small, according to Triffitt, who found it to measure 23μ.

Bionomics

Duffield (1927) removed a hundred females of *Heterodera* from the roots of hops every week for three years, and came to the conclusion that only one generation is produced in a year. He found that in March most of the eggs in the cysts were embryonated. The larvae hatch from April to July, and the first white females appear on the hop roots in the middle of June. They become brown by the beginning of August. White females have been found on hop roots as late as the beginning of November in Hampshire.

Nothing is known of the reactions of the larvae in the presence of root diffusates.

Effect on Host

Since Duffield (1925) proved that " nettlehead " disease of hops is not caused by *Heterodera*, and that perfectly healthy hops may have at least one cyst per 2.4 in. of root, there has been no evidence of harm caused by this parasite of hops. No investigations have been published on the histology of infected roots.

Hosts

One other plant belonging to the same family as the hop, namely hemp (*Cannabis sativa*), has been recorded as infected by *Heterodera* (Hollrung, 1890a), and in the closely related family Urticaceae, the two nettles *Urtica dioica* and *U. urens* are also known to be hosts of a species of *Heterodera*. Filipjev assumed that, as these plants are nearly related to the hop, the nematode found on them was probably *H. humuli* in all cases. The writer has succeeded in infecting *U. dioica* with cysts of *H. humuli* removed from hops. Triffitt (1929c) found both *U. dioica* and *U. urens* infected in a field where *H. schachtii* was present on mangolds, and other weeds were also infected in the same field, but it cannot be assumed that the nematodes on the nettles were either *H. humuli* or *H. schachtii*. Petherbridge & Jones (1944) also record cysts of the sugar-beet type on *U. urens* growing on land infested with sugar-beet eelworm.

Control

Since it has been shown that apparently *H. humuli* causes no disease in its host, no attempt to control it has been made. All the varieties of hop examined by Duffield proved to be infected.

Distribution

H. humuli on hops has been recorded from most of the hop-growing areas in southern England. It was recorded in Germany (Köln, Göttingen) by Voigt (1894). Triffitt found nettles infected in the west of England, and Petherbridge & Jones found them in East Anglia. It is possibly this species which, according to Filipjev (1934), has been recorded on hemp in the Union of South Africa.

CHAPTER IX

HETERODERA PUNCTATA THORNE, 1928
THE WHEAT NEMATODE

This species was described by Thorne in 1928(b), having been found parasitizing wheat in Saskatchewan, Canada. The only record of its occurrence outside Canada is that of Franklin (1938a), who found it on the roots of the grasses *Agrostis stolonifera* L. (syn. *A. alba*) and *A. tenuis* Sibth., in Hertfordshire, England.

Morphology

Male.—Thorne describes the male as having, beneath each striation of the outer cuticle, a double striation of the subcuticle made up of rows of refractive dots. The lateral fields are so prominent as to be wing-like. The labial framework is well developed, and the mouth stylet has large basal bulbs. There appear to be five annular striations on the head (Fig. 12 (6)). The submedian salivary gland is conspicuous. There is a very short, rounded tail. The copulatory spicules are large, fairly slender and arcuate (Fig. 12 (5)): they end in a simple tip and the edges appear to be rolled, but the limb is not twisted: they were 34–35μ long in two specimens measured by the writer. In total length the males measured by Thorne were 0.9–1.3 mm., while the mean of ten measured by the writer was 1.076 mm.

Female.—The mature female differs from all other known species of *Heterodera*, except *H. rostochiensis* and *H. marioni*, in not having a prominent vulva. The outline of the cyst is quite smooth posteriorly, and if examined in surface view the vulva can be seen as a pore lying level with the general surface of the cyst, while at a distance of about one and a half times the diameter of the vulval aperture is a second opening into the cyst, of about the same size, which represents the anus (Fig. 14 (2)). The general shape of the cyst is ovoid with, of course, a narrow neck at the anterior end.

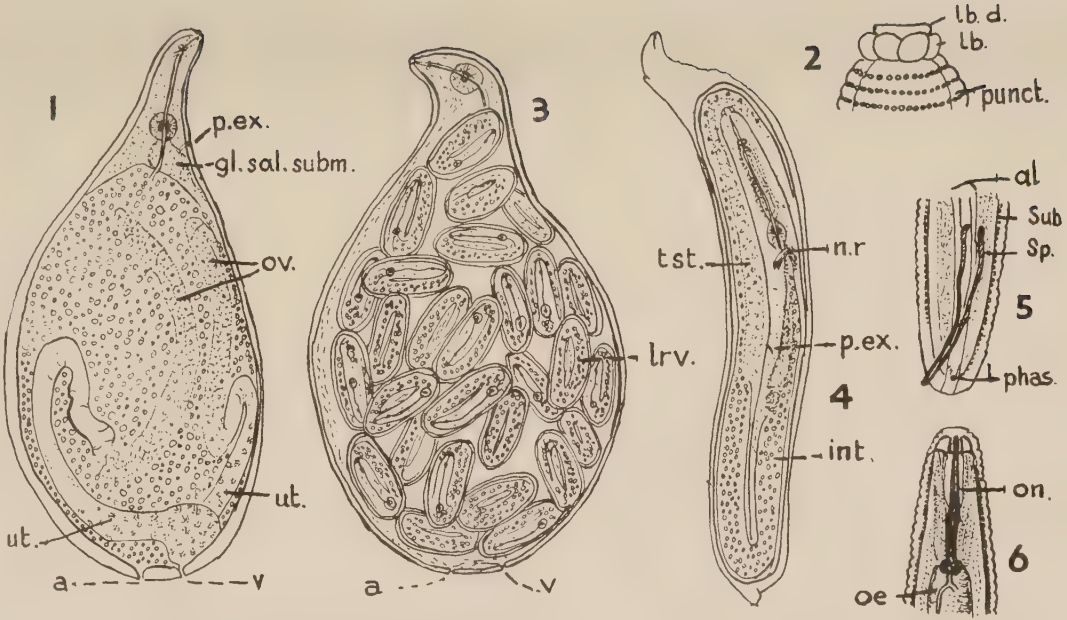


FIG. 12.—*Heterodera punctata*. (1) Immature female, × 25. (2) Lip region of female, × 2000. (3) Brown cyst filled with eggs containing fully developed larvae, × 125. (4) Mature male ready to moult for the last time, × 250. (5) Lateral view of male tail, × 750. (6) Head of male, × 750. (After Thorne.)

a. anus, al. wing, gl. sal. subm. submedian salivary gland, int. intestine, lb. lip, lb. d. labial disk, lrv. larva, n. r. nerve ring, oe. oesophagus, on. spear, ov. ovary, p. ex. excretory pore, phas. phasmids, punct. punctations of cuticle, sp. spicule, sub. subcuticle, tst. testis, ut. uterus with spermatozoa, v. vulva.

There is quite a conspicuous sub-crystalline layer on the newly formed cysts. In colour the new cysts are light brown or tan, and the wall is rather thin so that the eggs can be seen inside the cysts in many cases. Thorne gives the length as averaging 0.52 mm., while Franklin gives the length as 0.49 mm. (excluding the neck) and the breadth as 0.336 mm. The ratio of length to breadth is 1.479 to 1. Since the cysts are small, the number of eggs in them is not great : Thorne found about seventy-eight, while Franklin found the average in ten cysts to be one hundred and twenty-five. There is sometimes a small amount of jelly produced at the posterior end of the cyst, but eggs are seldom found in it [Fig. 13 (1)].

Eggs.—Although the cysts of *H. punctata* are small, the eggs are large compared with those of other species. According to the measurements given by Franklin, they are 123μ × 48μ, which is at least as big as those of *H. major*, the biggest form for which measurements have been given. They are also longer in proportion to their width than those of any other known species, the ratio of length to breadth being 2.56 to 1.

Larvae.—As might be expected from the size of the eggs, the larvae of this species are longer than those of any other species of which a large number of specimens have been measured. Franklin (1938a) gave the average as 0.55 mm., but subsequently (1940a), when a larger number had been measured, she gave a mean value of 582μ. Thorne (1928b) gives 0.35–0.47 mm. for the length of larvae from the Canadian population. The larval tail differs from that of any other *Heterodera* sp. in being more slender and more acutely pointed, so that this species can easily be distinguished in the larval stage [Fig. 13 (3)]. The stylet is about 26μ long. No other distinctive features have been described.

Bionomics and Effect on Host

In Canada, as described by Thorne (1928b), worms at all stages of development were found on wheat roots in the month of June. White females were present on the roots in August : on drying, these turned brown and were then found to contain embryonated eggs. In England, mature males and females of *H. punctata* were first found on the roots of bent-grass in May, while mature cysts with embryonated eggs were also found in October. No mention is made by Thorne of any damage caused to wheat by *H. punctata*, and the infections found in England on *Agrostis* spp. have been too light to have any obvious effect on the host.

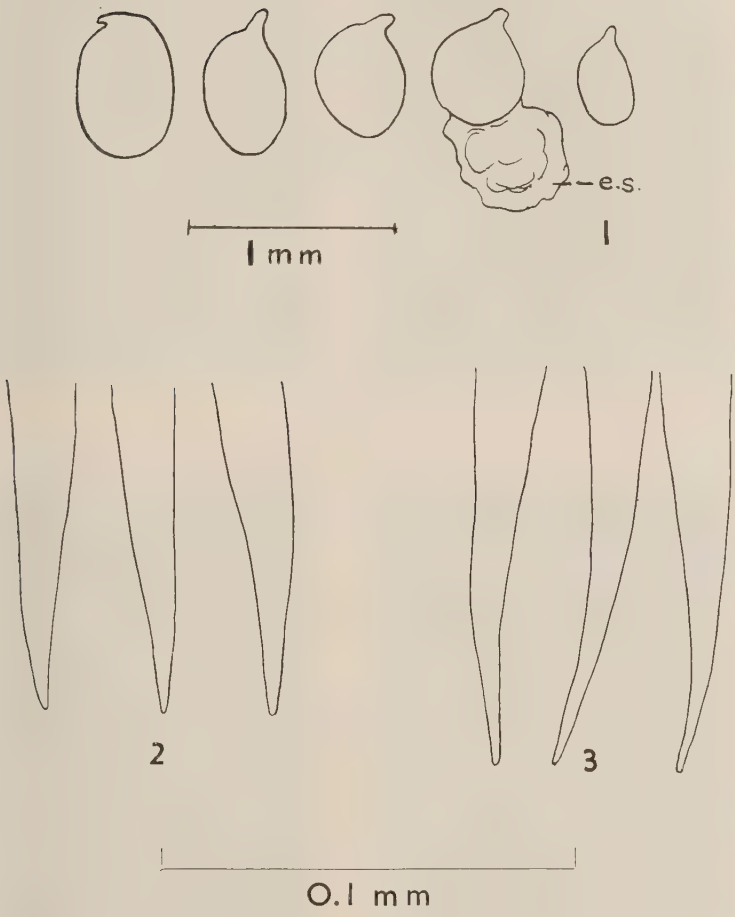


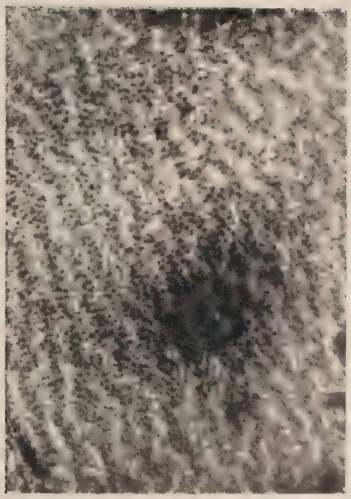
FIG. 13.—(1) *Heterodera punctata*. Cysts showing varying shapes and egg-sac (e.s.). (2) Outlines of larval tails of *Heterodera rostochiensis*. (3) Outlines of larval tails of *Heterodera punctata* showing more attenuated tips.

Hosts and Distribution

Besides wheat (*Triticum vulgare*), only two bent-grasses (*Agrostis stolonifera* and *A. tenuis*) have been found bearing *H. punctata* cysts, the wheat in Canada and the grasses in England. In Canada the nematode is present in Saskatchewan, where it was recorded nine times between 1927 and 1942, and in Alberta, where it was recorded from three districts between 1929 and 1942 (Baker, 1945a), in all cases on wheat. In England it was found on bent-grasses in Hertfordshire, but cysts of this species are of frequent occurrence in soils from many parts of Britain.

There is no published work on the control of this eelworm.

Fig. 14.—(1) Cyst wall of *Heterodera major* with irregularly arranged punctations. ×750. (2) Posterior end of cyst of *Heterodera punctata* showing approximately equal vulval and anal apertures and regularly arranged punctations (lower left-hand corner). ×500. (3) Cyst wall of *Heterodera rostochiensis* with regularly arranged punctations. ×750. (4) Posterior end of cyst of *Heterodera rostochiensis* with vulva (V) and small anus (A). ×500.



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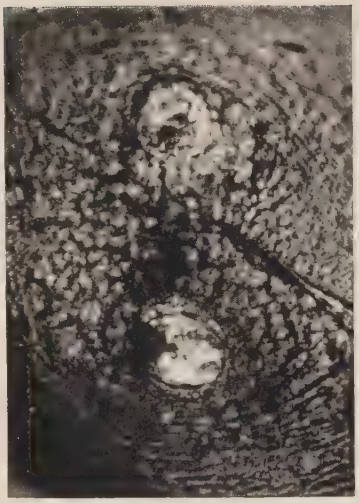

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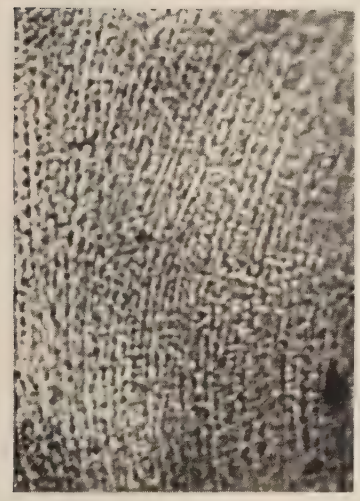

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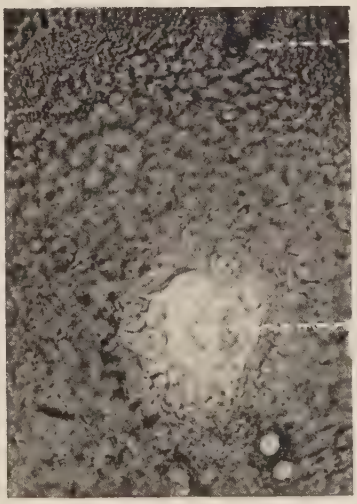

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FIG. 14

FIG. 15.—Bad patch of " potato sickness " due to *Heterodera rostochiensis*. (By courtesy of School of Agriculture, Cambridge.)

CHAPTER X

HETERODERA ROSTOCHIENSIS WOLLENWEBER, 1923

THE POTATO ROOT EELWORM

Syn. *H. schachtii* forma *solani* Zimmermann, 1927
H. schachtii subsp. *rostochiensis* (Woll.) Kemner, 1929

The first to record cyst-forming nematodes of the genus *Heterodera* on potatoes was Kühn (1881), who attributed the attack to *H. schachtii*. This was, however, an isolated observation, and ten years later both Kühn (1891) and Hollrung (1890a), classed solanaceous plants as insusceptible to attack by this eelworm. Vaňha & Stoklasa (1896) also considered potatoes to be immune, but both Hiltner (1909) and Marcinowski (1909) stated that the sugar-beet nematode could parasitize the potato—apparently without having seen it, according to Goffart (1934a, p. 73). Zimmermann (1914) was the first to declare quite definitely that the potato could be parasitized and severely damaged by *Heterodera* although, as only one cyst-forming species was then recognized, the attack was attributed to the sugar-beet eelworm. In Britain the disease first began to cause trouble at about the same time : Massee (1913) recognized it as a common parasite of potatoes in Scotland, while Strachan & Taylor (1926) say that it occurred in Yorkshire in 1904, and Warburton in 1919 reported its occurrence in several places. Other outbreaks of eelworm disease of potatoes were observed in the 1920's, showing that by then the parasite was already widespread.

In Ireland (Carroll, 1933a) and Sweden (Kemner, 1929a) the disease was first noted in 1922, and by 1928 (Denmark, 1929) it had become known in Denmark. Eight years later two small outbreaks were observed in the area of intensive early potato culture in Jersey (Small, 1939), and more recently (Cannon, 1941 ; Chitwood, Clement, Morgan & Tank, 1942) the potato root eelworm

has been discovered in one area of Long Island, U.S.A. In all the European countries where it occurs the potato eelworm has continued to spread and cause considerable damage, both on a field scale and in gardens and allotments, particularly in areas where potatoes are cultivated year after year.

The first worker to recognize morphological differences between the sugar-beet eelworm and the potato root eelworm was Wollenweber (1923). On account of the shape of the cyst and the size of the larvae and larval mouth stylet, as compared with those of *H. schachtii* and *H. marioni*, he considered the potato-infesting form to be a distinct species and named it *H. rostochiensis*. Kemner (1929a) refers to it as *H. schachtii* subsp. *rostochiensis*, and Zimmermann (1927) calls it *H. schachtii* forma *solani*, as neither author considered it to be specifically different from *H. schachtii*. Goffart (1928), Triffitt (1928) and Reinmuth (1929) all agreed that the potato root eelworm should be regarded as merely a specialized strain of the sugar-beet nematode. However, in 1940 Franklin (1940c) described morphological differences between the potato and the sugar-beet eelworms which were sufficiently well marked to justify the separation of the potato " strain " as a definite species, and Wollenweber's name, *H. rostochiensis*, was restored.

Morphology

Male.—The average length of 100 males of *H. rostochiensis* measured by Franklin (1940c) was 1.113 mm., which is not very different from that of several of the other species, though rather shorter than males of *H. schachtii*. The stylet is 27–28μ long. The characteristic feature is in the copulatory spicules : they are rather slender, about 34μ long, and the tips end in a single point which appears to be more delicate than the main limb of the spicule (Fig. 16 (1) . In general form they are not greatly different from those of the other species of *Heterodera*. The annulations on the head of the male appear to be distinctly finer and more numerous than in most other species. Owing to their narrowness it is not easy to be sure of the exact number, but there are probably five or six, and in some cases there appear to be eight or nine. No other anatomical features characteristic of the males of *H. rostochiensis* have been described.

Female. The female is very characteristic in that there is no prominent vulva in the mature worm or the cyst. The posterior

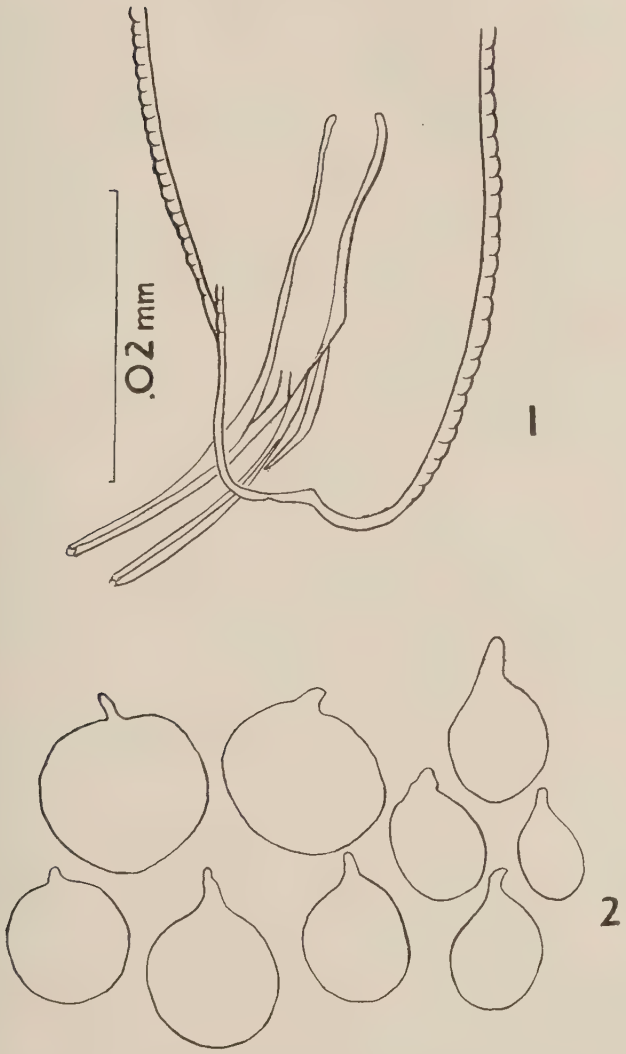

FIG. 16.—*Heterodera rostochiensis*. (1) Tail of male showing shape of spicules. (2) Cysts of various shapes (after Triffitt).

end is rounded, and the vulval aperture can be seen as a small terminal opening. At a little distance from it, it is possible to see the anus as a considerably smaller aperture [Fig. 14 (4)]. The only other species of *Heterodera* in which the mature female has a smoothly rounded posterior are *H. marioni*, where the female does not become a brown cyst, and *H. punctata*, in which there is a cyst but in which the two apertures, vulval and anal, can be seen fairly close together and approximately equal in size. *H. rostochiensis* can thus be fairly easily distinguished by the structure of the posterior end of the cyst. In shape the cysts are very nearly spherical, and the neck is sharply offset and fairly long. Goffart (1930a) gives the mean length of the neck as 100μ, while in cysts from oats the mean is 52μ, and from sugar-beet it is 67μ. The ratio of length (excluding the neck) to width of the cysts is given by Goffart as 1.038 to 1, while the writer found it to vary between 1.04 to 1 and 1.09 to 1. Small cysts formed late in the season from females which have had their period of development curtailed are much more elongated, and might be described as pear-shaped [Fig. 16 (2)].

The actual size of the cysts varies considerably, and very different measurements have been given by different workers. Wollenweber (1923) gives 0.835 mm. × 0.694 mm., Kemner (1929a) 0.631 mm. × 0.513 mm., Goffart (1930a) 0.610 mm. × 0.491 mm., and Triffitt (1928) 0.576 mm. × 0.405 mm. There is evidence that the host and the texture of the soil have an influence on the size of the cysts (Gemmell 1940, Boyd 1943a).

The cyst wall of *H. rostochiensis* is usually fairly thick, and is covered with minute punctations which are arranged in rows running latitudinally round the cyst (Franklin, 1939c). The rows are not quite regular, and are often broken, but the general arrangement of the punctations is predominantly in rows [Fig. 14 (3)]. On maturing the white female first becomes bright yellow, then changes through a golden brown to tan, and finally to a rich chestnut brown. These changes have been shown by Ellenby (1946c) to be brought about by the enzyme polyphenol oxidase, and to be fundamentally the same as the process which occurs in the browning and hardening of insect cuticle. Unlike insect cuticle, the cyst wall has no outer waxy layer which would render it impermeable to water. Ellenby (1946c) showed that a large cyst can lose its own volume of water in 10–15 minutes through the cyst wall if the vulval aperture is blocked. In the yellow phase the colour is not in the cyst wall

itself but in the contents, and shows through the wall, which is not very thick at this stage. The yellow phase has given rise to the name "golden nematode of potatoes", which is the accepted popular name for the potato root eelworm in the U.S.A. There is no sub-crystalline layer : occasionally on young females it is possible to see the remains of the cast larval cuticles, but by the time the worm has reached its full size there is no trace of any encrusting material like that occurring on cysts of *H. punctata* and *H. major*.

In other morphological features the females of *H. rostochiensis* resemble those of other species of the genus. The mouth stylet measures 24–26μ. There is no egg-sac. The numbers of eggs per cyst vary with the size of the cyst from under 50 to 500–600.

Eggs.—These are of the usual shape, without any tendency to be barrel-shaped (cf. *H. göttingiana*). Kemner (1929a) gives the size as 103μ × 48μ, Goffart (1930a) as 101.8μ × 41.2μ, and the writer (new observation) as 101.4μ × 46.7μ. The ratio of length to breadth is thus over 2 to 1 (varying from 2.17 to 1 to 2.47 to 1), whereas in *H. göttingiana* it is less than 2 to 1.

Larvae.—These are typical in form and of medium size. The length has been given variously as 372μ (Wollenweber, 1923), 444μ (Kemner, 1929a), 445μ (Goffart, 1930a), 468μ (Reinmuth, 1929) and 458μ (Triffitt, 1928), and the writer has found it to vary between 450μ and 460μ. The larvae are thus probably a little shorter than those of *H. schachtii* and *H. göttingiana*, which usually average 470–500μ, much shorter than those of *H. major* and *H. punctata* (570–580μ), but longer than those of *H. cruciferae* (418μ) and *H. humuli* (380–400μ).

Bionomics

The development of the potato root eelworm has been studied by Miles (1930) in England, by O'Brien & Prentice (1930) in Scotland, and by Chitwood & Buhrer (1946a,b) in America. They all agree that the time taken for mature females to develop from the larvae is five to six weeks. Chitwood & Buhrer say that there is no larval ecdysis within the egg, but that the first-stage larva hatches from the egg, leaves the cyst and makes its way through the soil to the potato root, which it enters close to the tip. The larva crosses the cortex to the endodermis, where it comes to rest lying parallel with the long axis of the root, as in the other species of *Heterodera*.

The first ecdysis takes place in a few days, and the second in a further two or three days. The third-stage larva is considerably more plump than the first [Fig. 17 (4)], but is about the same length. Chitwood & Buhrer consider that the sexes can be distinguished at this stage, and certainly by the end of the third stage about ten days later, when the rudimentary paired ovaries can be seen in the female [Fig. 17 (5)], and in the male the single testis has begun to develop and the rectum has thickened. In both sexes the body swells considerably, and if the invaded root is a thin one the posterior part may protrude through the cortex to the exterior. The fourth stage of larval development also lasts about ten days, and during it the female continues to swell rapidly, so that by the fourth moult she becomes pyriform or flask-shaped, with the hind end protruding through the root and visible to the naked eye. By this time the male has also assumed the adult form and is again worm-like, coiled within the fourth larval cuticle, and usually lying exposed on the root surface. During the fourth stage the copulatory spicules develop in the male, and in the female the transparent larval cuticle has taken on the opaque pearly-white appearance which makes the young adult easily visible to the naked eye. Soon after the fourth moult the male escapes from the ensheathing cuticle and becomes free in the surrounding soil [Fig. 18 (6)]; he finds a mature female and fertilization takes place. The ovaries of the fertilized female then develop rapidly, ultimately filling practically the whole of the swollen body, and eggs may soon be distinguished. These begin to segment at once, and three or four weeks after fertilization the cyst is full of embryonated eggs. Meanwhile the female has died and the cuticle has become tough and brown, as described above.

According to Miles (1930), mature females may be found on the roots of potatoes growing in infested soil after about six weeks' growth, and fully developed larvae in the cysts in another month. In Scotland, according to O'Brien & Prentice (1930), about the same time is required, while the male takes 6–7 weeks to develop. The period from larva to larva under the conditions in Long Island, where the soil temperature averaged 63° F. during the observations made by Chitwood & Buhrer, was 38–48 days. That temperature

FIG. 17.—*Heterodera rostochiensis*. Development of female. (1) Infective larva (sex undeterminable). (2) Larva undergoing first moult. (3) Early phase of second moult. (4) Third stage larva moulting. (5) Fourth stage before final moult. (6) Adult female after fourth moult. (All after Chitwood and Buhrer, × about 170.)

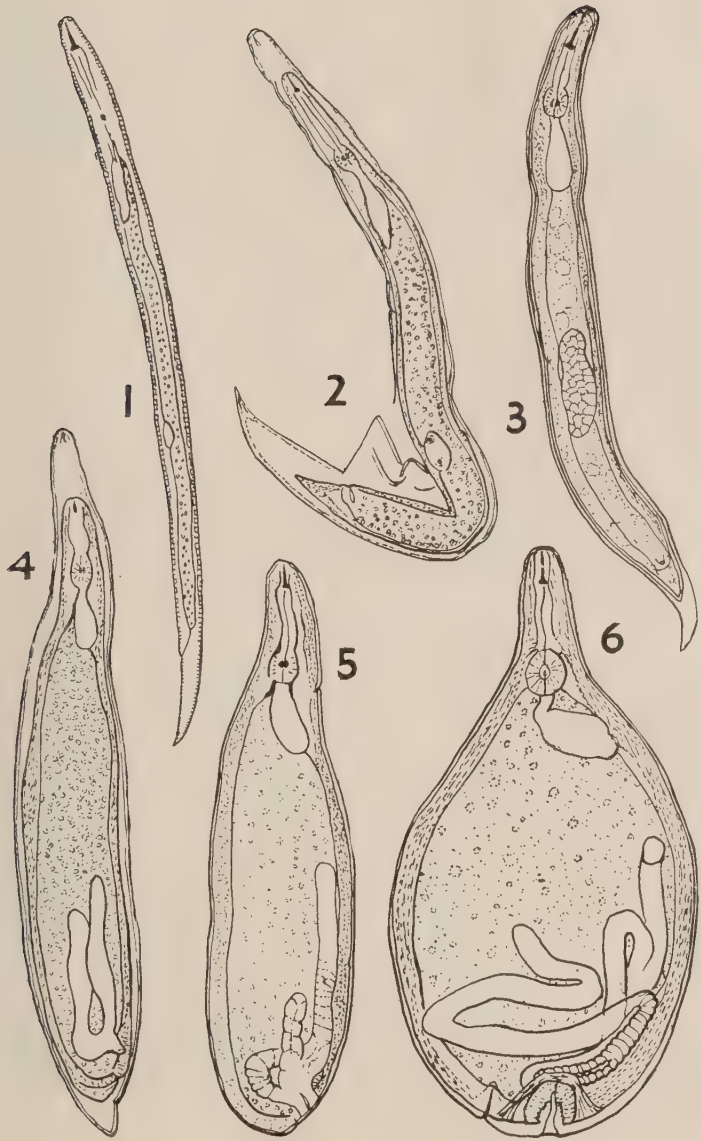

FIG. 17

influences the rate of hatching of larvae was shown by Miles, who found a relationship between the numbers of larvae invading potato roots and the temperature of the soil, but he states that the rate of development of the parasite within the roots was practically uniform throughout the season. Chitwood & Buhrer (1946a,b) also investigated the effect of temperature on the entry of larvae into potato roots. They say that there is little activity of the larvae below 55° F., but that at 59°–60° F. there may be mass invasion.

A very striking feature of the bionomics of the potato root eelworm is the way in which it responds to the presence of growing potatoes. The larvae hatch from the cysts in very small numbers, or not at all, so long as no potatoes are growing in the vicinity, but in the presence of living potato roots, which are assumed to give out some stimulating chemical, the larvae hatch in large numbers. This was shown in laboratory tests by Triffitt (1930a), O'Brien & Prentice (1930) and Carroll (1933b). The activating agent has generally been referred to as "potato root excretion", but the term "diffusate" is more appropriate and has now been adopted. The chemical composition of the substance has been investigated by Todd *et al.* (1947) and Marrian (1948). Some of its biological properties were first discovered by Triffitt (1930a). She found that it is to some extent heat-resistant, is non-volatile, and remains active in sterile solutions for some considerable time. It stimulates hatching even in very dilute solutions. Ellenby (1944b) measured the oxygen consumption of living potato roots immersed in water, which he assumed to be a measure of their rate of metabolism and consequently of their production of root diffusate, and used this value to standardize diffusates from various species of *Solanum*. That potato eelworm larvae are stimulated to hatch by diffusates from the roots of other members of the family Solanaceae besides potatoes was shown by Franklin (1940a). In laboratory hatching tests she found that larvae hatched in large numbers when the cysts were soaked in diffusates from the roots of tomato (*Lycopersicon esculentum*), black nightshade (*Solanum nigrum*), woody nightshade or bittersweet (*S. dulcamara*), winter cherry (*S. capsicastrum*), and deadly nightshade (*Atropa belladonna*). Diffusates of grasses, oats and maize

FIG. 18.—*Heterodera rostochiensis*. Development of male. (1) Larva in early phase of (2) second moult. (2) Third-stage larva. (3) Third-stage larva moulting. (4) Early fourth-stage male beginning to coil within third cuticle. (5) Fourth-stage male beginning to moult. (6) Adult male. (All after Chitwood and Buhrer, × about 170).

FIG. 18

did not cause hatching in these experiments.

Even when a potato crop is grown all the larvae do not hatch from the cysts in the surrounding soil, but the precise reason for this is not known, nor is it known what proportion of the larvae do hatch. To some extent the rate of hatching varies with the season of the year, but this does not account for all the variations observed. Since very few larvae hatch in the absence of the host plant or of certain closely related plants, the cysts do not become empty, even after several years; it follows that once a soil is infested with potato root eelworm, it is practically impossible to get rid of the infestation simply by waiting for it to die out naturally, even though there is little danger of weeds acting as reservoir hosts. An infested soil which has been free from potatoes or tomatoes for seven years still contains cysts with some viable eggs in them, and a heavy infestation is soon restored when the host plant is again cultivated (Miles & Miles, 1942).

A possible explanation of this failure of all the larvae in a cyst to hatch at the same time was put forward by Ellenby (1946d). He observed that a greater proportion of the larvae would hatch from cysts which had been punctured before being placed in potato root diffusate than from undamaged cysts. He also found that if the cysts were pre-soaked in acid solutions, the numbers of larvae which would hatch subsequently in potato root diffusate were reduced more or less according to the *p*H of the acid solution used, although the cysts were washed for twenty-four hours after being removed from the acid. From these observations he concluded that the cessation of hatching from untreated cysts before all the apparently mature larvae had emerged is due to the accumulation inside the cyst of some inhibiting substance, which is normally dispelled gradually, but disappears quite quickly when the cyst is punctured. If such a substance exists, he thinks that it may be of an acid nature. The hypothesis of an inhibiting substance may help to explain the variable hatching rate which has been observed.

In investigating the effects of lethal agents on cysts of *H. rostochiensis*, it is necessary to be able to tell whether or not treated cysts contain larvae still capable of hatching. When the composition of the stimulating principle in potato root diffusate was still unknown, various chemicals were being tested in the hope of finding some artificial stimulant which could be used *in vitro* for testing the viability of cysts. Smedley (1936) found that calcium

hypochlorite at low concentrations (1 in 7,500 to 1 in 4,000 available chlorine) stimulated hatching, although higher concentrations were lethal. Fenwick (1943b) said that picric acid was effective at concentrations of 0.01–0.02%. Boyd (1943b) stated that if cysts were pre-treated for a short time in dilute solutions of certain organic silver compounds such as 0.001% silver proteinate, and then placed in potato root diffusate, greater numbers of larvae hatched than from cysts which had not been pre-treated in any way. Cysts treated with higher concentrations and for periods of two or three weeks or more were in many cases killed.

Exposure of the cysts to the action of earthworms also apparently makes the larvae more ready to hatch in potato root diffusate. Ellenby (1944a) found that cysts from soil in plant pots containing numbers of earthworms, and cysts from worm casts, produced more larvae per cyst, the larvae hatched sooner, and a greater proportion of the cysts produced larvae. Apparently cysts were unharmed by passage through earthworms, and it appears (Ellenby, 1946d) that it is the digestive enzymes in the gut which act on the cysts and cause increased hatching. This increased vitality appears to last for some months at least, since the cysts were kept in moist soil with earthworms from November to February, when some of the soil was removed and dried, the cysts were extracted, and the hatching tests were carried out in the following June.

Triffitt (1929b) fed eelworm cysts to young pigs, but found that after passage through this animal they were no longer viable.

Boyd (1941) tried to find a means of testing free larvae in the laboratory to discover whether they are alive or not. Living larvae may remain motionless in water for a considerable time without any indication of their viability, which makes it difficult to determine the effectiveness of lethal agents. Boyd found that under certain conditions he could distinguish dead from living larvae by the yellow colouring of the former when immersed for a time in dilute iodine solution, while living larvae remained unstained until they had been killed by the iodine.

The effect on larval hatching of immersing *H. rostochiensis* cysts in mixed root diffusates from potato and six different species of cruciferous plants was studied by Ellenby (1945a). When root diffusates of cress, white mustard and black mustard were mixed with the potato root diffusate, hatching was much less than in potato root diffusate alone. Except after exposure to cress root

diffusate, the effect did not persist when the cysts were removed to pure potato root diffusate. Dilute solutions of allyl isothiocyanate (the mustard oil of black mustard) when added to potato root diffusate produced similar results.

The effects of freezing cysts and larvae of the potato root eelworm were investigated by Boyd (1943a). The free larvae were easily killed by freezing, but results when cysts were frozen were variable. He also investigated the influence of soil conditions and found that cysts produced on the roots of potatoes growing in pure clay were smaller and less productive of larvae than others developed on plants growing in pure sand. Very curiously, in Boyd's experiments no cysts were developed on potatoes grown in pots of peat-moss litter infected with eelworm larvae in just the same way in which the sand and clay were infected. No explanation was offered for this occurrence. Robertson (1937) also describes differences in numbers and morphology of cysts produced on potatoes growing in experimental plots of different soil types.

Gemmell (1940) observed differences in the size of the cysts and in the numbers and rate of hatching of larvae, between two populations of cysts obtained from two fields in the same locality. He found that when these two populations produced another generation under identical experimental conditions and on the same variety of potato, although the difference in size practically disappeared, the differences in numbers and rate of hatching of the larvae were maintained. Gemmell therefore concluded that phenotypic or even genotypic races of the potato eelworm exist, having differences in the size and productivity of the cysts.

Effect on Host

The symptoms of eelworm disease of potatoes have been described by many authors (e.g. Kemner, 1929a; O'Brien & Prentice, 1930; Goffart, 1936a; Morgan, 1925, 1926). The first sign of unhealthiness is shown by a halt in normal development when the tops are a few inches high; the lower leaves of the affected plants then begin to wilt and die, and the other leaves assume a dull unhealthy colour. There is a marked tendency to wilt, and the upper leaves soon begin to show brown patches at the tips of the

Fig. 19.—Potato plant infected with *Heterodera rostochiensis* showing "feather duster" appearance. (By courtesy of School of Agriculture, Cambridge.)

FIG. 19

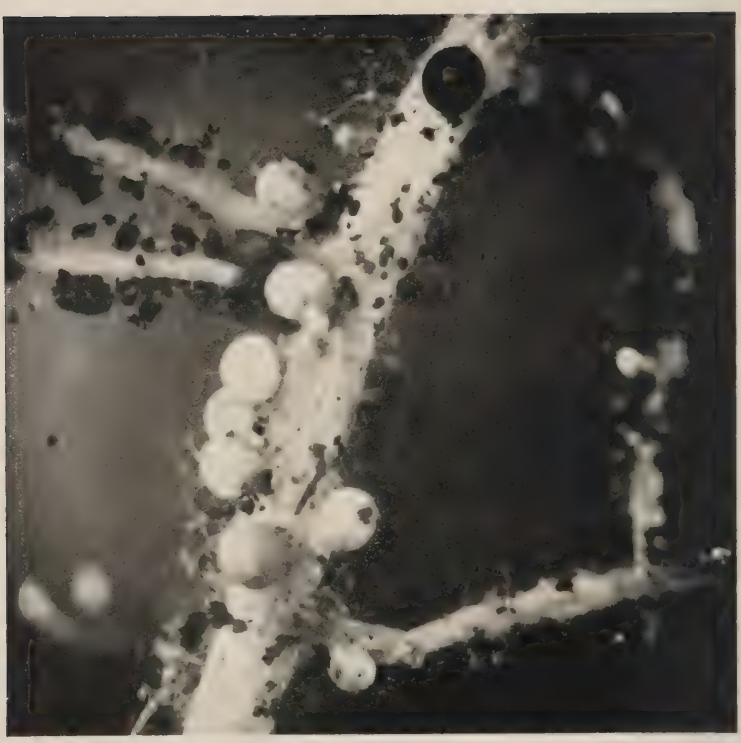

FIG. 20.—Potato root bearing eelworm cysts of different ages. Greatly enlarged. (By courtesy of School of Agriculture, Cambridge.)

leaflets and along the margins, and then to turn prematurely yellow. The roots are brown and unhealthy in appearance, and abnormally branched (Fig. 19) ; the plant has somewhat the appearance of a feather duster. In severe attacks many of the roots are destroyed at the tips and consequently are shorter than the normal. When the plants have been growing for about eight weeks or a little less, the female nematodes may be seen on the roots as minute white, then yellow, and finally brown beads, with a diameter of one-half to three-quarters of a millimetre (Fig. 20). The whole plant dies down prematurely, the tubers are small and the crop much reduced. These macroscopic symptoms are largely due to the injury caused to the roots by the entry and development of the nematode larvae, and to the formation of giant cells which disturb the translocation system of the plant in the same way as in sugar-beet roots parasitized by *H. schachtii*. As far as is known, the histological changes in the potato root (Fig. 21) take the same course as in the infected sugar-beet root (Triffitt, 1931a).

Diseased plants usually appear at first in isolated patches in a field, and if potatoes continue to be grown the patches become larger each year until finally the whole field is affected (Fig. 15). The spread of the patches is due largely to the mechanical spread of the eelworm in the course of the cultivation of the ground. A very puzzling feature of the disease, often observed and recorded, is that a plant may carry a large number of cysts on the roots and yet appear quite healthy and give a normal yield. This frequently occurs outside the bad patches in infested fields, or in an infested field which has been rested from potatoes for four or five years or more. It has been suggested that the disease is the result, not of eelworm attack alone, but of a combination of some other factor or factors acting in association with the parasite.

Miles (1930) observed four separate cases where normal potato crops were produced in 1929 on land where a potato crop had failed in the previous season. In all of them there was a high concentration of cysts in the soil, and a severe attack by the root fungus *Corticium solani* early in the season. In adjacent fields, with apparently identical conditions, the plants were diseased from the outset and the symptoms were typical of eelworm disease. No explanation of these differences could be given. Miles found a correlation between the numbers of cysts in the soil and on the roots of the potato plants growing in it, but no apparent relationship between the appearance

and yield of plants grown in pots and the intensity of infestation of the soil in which they were grown. In field-grown potatoes the two root fungi *Corticium solani* and *Colletotrichum tabificum* were very frequently observed, both in the presence and in the absence of eelworms. The former fungus may give rise to a pathological condition known as "stem canker", but this is usually temporary, and the plants recover from it even when eelworm is also present. *Colletotrichum tabificum* is considered to be saprophytic, and to hasten the dying of the potato roots in autumn; normally it is probably not harmful, and cannot be considered by itself to give rise to symptoms of disease.

Buckhurst & Fryer (1931), as a result of investigations extending over two years on plants both in the field and in pots, concluded that while the disease does not occur in the absence of the nematode, it need not be manifest in heavily parasitized plants. In fact, no correlation was found between the number of cysts in the soil and the intensity of the disease. No parasitic organism other than the eelworm could be found which appeared to be capable of causing the disease. The experiments led these authors to believe that the disease is due to eelworm attack coupled with a soil factor which prevents the vigorous early growth of the potato roots. They suggest that the second factor is some nutritional defect not rectified by normal manurial practices.

Carroll (1933a,b) and Carroll & McMahon (1935, 1937) have investigated the causes of potato sickness in Ireland. They also observed that symptoms of disease might be absent from heavily infected plants, and that certain fungi, notably *Rhizoctonia solani*, might be present on the potato roots. They grew potatoes in pots of soil which had never grown potatoes and to which eelworm cysts in various quantities had been added, and also in "potato-sick" soil from which cysts had been removed by sieving. As a result of their observations they conclude: "It appears obvious therefore that potato sickness is caused by the attack of the potato eelworm and that the intensity of the disease is influenced very much by the number of eelworms present in the soil" (Carroll, 1933b, p. 151); also, "there is a definite relationship between the cyst content of the soil (meaning cysts containing viable eggs) and the intensity of potato sickness in all cases where the cyst content of the soil is not greater than about 3 or 4 per c.c. It has moreover been observed that about 4 cysts per c.c. can give rise to potato sickness in its most severe form and accordingly there cannot be a relationship between the cyst

content of soil and intensity of disease when the cyst content rises above 4 per c.c." (Carroll & McMahon, 1935, p. 79).

In other experiments, Carroll & McMahon (1934, 1935, 1937) grew potatoes in sterilized soil to which were added large numbers of eelworm cysts. It was shown that steam sterilization of the soil had some effect on the potato root diffusate, causing its neutralization, so that it did not stimulate the eelworm larvae to hatch as soon as they would normally have done. The result was that plants growing in sterilized soil reinfected with cysts were able to make some growth before becoming infected, and showed no symptoms of

FIG. 21.—Transverse section of potato root infected with *Heterodera rostochiensis* showing formation of giant cells (g.c.) : 45 days after infection. × 80. ph. phloem, xy. xylem, y.c. young cyst. (From O'Brien & Prentice.)

disease although they eventually bore a heavy infection. It is suggested that when plants in the field are found bearing many cysts but apparently healthy, it may be due to some factor which enabled them to become well established before the initial attack by the nematodes. This theory is thought to explain the fact that early potatoes at Rush, County Dublin, though infected, usually grow well : it is assumed that they become established early in the year when the temperature is too low for the eelworms to have begun mass invasion of the roots. Potatoes grown later in the same ground often fail completely. This theory is supported by observations made by Chitwood (1945) and by Chitwood & Buhrer (1946a,b) on soil temperatures in spring, correlated with the rate of growth of potato roots at different temperatures, and with the temperature at which nematode invasion is at its height. Further support is given by the fact that early potatoes succeed on heavily infested ground in south-east Scotland (O'Brien & Prentice, 1930), where there are probably the same conditions of early growth of potatoes before the soil temperature has risen sufficiently for the nematodes to become very active. In Cornwall the disease is very destructive in the early potato districts, and it seems likely that here the soil conditions are warmer when the plants start to grow, so that the eelworms are active from the beginning and invade the roots as soon as they are put out. The same result would occur, on the other hand, if the *Heterodera* population in Cornwall were capable of becoming active at lower temperatures than most other populations.

The fact that if " potato-sick " land is rested from potatoes for two or three years, the first subsequent crop of potatoes will usually yield quite well although heavily attacked by eelworm, can probably be accounted for on the same theory, since the invasion of roots by larvae from cysts which are more than one year old does not take place quite so rapidly as from one-year-old cysts (Franklin, 1938b).

Of the soil factors other than temperature which might contribute to the production of potato sickness, only that of the *p*H value of the soil has been investigated to any extent. This was studied by Peters (1926) in relation to the cyst content of the soil. In an experimental field he found a correlation between the *p*H of the soil solution and the cyst concentration, but after further investigations Morgan & Peters (1929) decided against this conclusion, and Carroll (1933b) also found no relationship between these two factors

Kemner (1929a) found that composition and *p*H of the soil had little influence on the intensity of nematode infestation. O'Brien & Prentice (1930), looking for some effect of soil *p*H on severity of disease and on cyst content, found no relationship in either case. It thus seems fairly clear that only in so far as soil reaction affects the growth of the potato plant does it influence the nematode.

It has been suggested that the disease symptoms produced in the potato when invaded by *Heterodera* might be caused by the production of some kind of harmful toxin by the parasite. There is no proof of this, but if there were it would be difficult to explain the healthy appearance of some heavily infected plants, unless it be assumed that for some reason certain plants could withstand the effects of the toxins better than others. No other explanation for the phenomenon of heavily infected plants appearing healthy has been suggested, and Carroll & McMahon's theory remains the most probable.

Goffart (1938a) studied the problem of potato sickness, and agreed with the British workers in concluding that the root fungus *Rhizoctonia solani* does not play a significant part in causing the disease. He considers that, in addition to the eelworm, there is some " factor of depression " playing a secondary part in the disease. This factor, which is probably a metabolic upset due to the eelworms, can be mitigated by increasing the amount of nitrogen in the soil. Goffart observed variations in sprouting and a decrease in the starch content of tubers grown in infested soil, and also some irregularity in the fermentative processes in the tubers, resulting in quicker and more intense discoloration of the cut tuber tissue than normally takes place. The *p*H of potatoes from infested soil was often found to be higher than that of those grown in uninfested soil.

Estimation of Soil Infestation

Before mention is made of the various attempts to find means of eliminating the losses caused by potato sickness, some of the methods which have been evolved for estimating the eelworm population of the soil will be briefly described. In order to find out whether a soil is infested with *H. rostochiensis*, it is most convenient to determine whether cysts are present, since it is the resistant cystic stage which carries over the infection from year to year. As it is practically impossible to pick out the brown cysts from soil by hand, Morgan (1925) devised a method of shaking samples of dried soil with water and

pouring off the scum which floats up, and in which the cysts are found. The scum may then be dried and the cysts picked out from it and counted. As most potato eelworm cysts are nearly spherical, a large proportion of them may be rolled out from amongst the other dried débris on a smooth, gently sloping surface such as a sheet of stiff paper, if this be lightly tapped. The number of cysts in a given weight or volume of soil may be found by this method, since it may be assumed that most of the cysts are removed from dried soil by flotation in water. Kemner (1929b) worked on the quantitative estimation of several species of *Heterodera* cysts in soil, and Fenwick (1940) elaborated and improved Morgan's method. It was however always recognized that the number of cysts present was not directly proportional to the numbers of infective larvae in the soil, since the cysts are of varying ages and sizes and hence contain very different numbers of larvae, and many cysts are empty. Triffitt (1934) supplemented the information given by cyst counts by dissecting a number of cysts from each sample and estimating whether they were full, three-quarters full, half full, one quarter full or empty. Direct estimation of the numbers of larvae in the cysts removed from a known sample of soil was made by Fenwick (1942b), who obtained the larvae from the cysts by chemical means (i.e. by solution of the cyst walls). The larvae may, of course, be counted after having been caused to hatch by the use of root diffusates of potatoes or tomatoes as in the experiments of Fenwick (1943a) and Ellenby (1943).

Another method of determining the infective potential of infested soil is that used by Gemmell (1939), who stained the roots of potato plants growing in the soil being investigated, and observed the numbers of *Heterodera* larvae present in them. This method has been employed in a slightly different form by Franklin (1938b). It is useful for showing the relative infectivities of a number of soils but, as so far employed, does not measure the absolute infectivity. Some workers (Triffitt, 1929a ; Hurst & Triffitt, 1935b) have counted the cysts formed on the roots of potatoes growing in plant pots full of the soil under test. When the females are mature, the ball of soil and roots is turned out of the pot in one piece, and the cysts visible on the roots appearing on the surface of the ball of soil are counted. This method has certain advantages over the others since only those larvae which are capable of infecting the host and coming to maturity on its roots are counted. However, it takes rather a long time, and takes no account of those larvae which have developed into males

and have wandered away in the soil by the time that the cysts are formed, nor of cysts on the unexposed roots. Other workers have estimated the numbers of young females present while they are still at the " white cyst " stage (Reinmuth & Engelmann, 1942 ; Chitwood & Feldmesser, 1948).

Control

Intensive research has been undertaken into various possible methods of combating potato sickness. On the one hand, the eelworm itself has been attacked in the soil by means of lethal chemicals and by artificial hatching stimulants. On the other hand, attempts have been made to help the potato to resist disease by stimulation with fertilizers, by cultivation methods, and by a search for immune varieties.

Chemical Methods.—Reviews of the work done in Britain on the control of *H. rostochiensis* with chemicals have been given by Hurst & Triffitt (1935b), and more recently by Miles & Miles (1946). Various chemicals such as bleaching powder, sulphur, limestone, drained creosote salts, calcium cyanide, calcium cyanamide, and naphthalene have been applied to " potato-sick " land, and a crop of potatoes then grown. In some cases, e.g. after naphthalene (Morgan, 1925 ; Roebuck, 1928 ; Miles, 1930 ; Buckhurst & Fryer, 1931) and drained creosote salts (Edwards, 1929), the potatoes were healthier and gave an improved yield, but there was apparently no reduction in the eelworm population of the soil. Carbon disulphide, calcium cyanide and calcium cyanamide were found by some workers to produce some improvement in the crop, but the dressings of any of these chemicals necessary for adequate control of the disease would be so heavy as to be economically impracticable. Since 1935 intensive tests of calcium cyanamide have been described by Hurst & Triffitt (1935a,b ; 1937), Hurst (1938a,b), Hurst & Franklin (1937 ; 1938a,b), and Edwards (1937a), while Smedley (1939) and O'Brien, Gemmell, Prentice & Wylie (1939) found that chloroacetates were lethal to eelworms in laboratory tests, and calcium and ammonium chloroacetates showed some degree of control when used on a small scale in the field. Calcium chloroacetate was also used by Edwards (1939a) and by Gemmell (1944) in field experiments, but it did not reduce the infestation of the soil and it checked the early growth of the potatoes. A compre-

hensive experiment in the chemical control of potato sickness was carried out by Miles, Henderson & Miles (1943), who tested gasworks liquor, calcium cyanamide, calcium chloroacetate, farmyard manure and artificial fertilizers over a period of three years at six centres and with four varieties of potato. No striking degree of control was achieved, as measured by yield. It was found (p. 156) that "Data . . . suggest that a high viable cyst concentration is only maintained when the yield [of potatoes] is maintained at the level of that obtaining when the original infestation was produced. A fall in yield seems to be associated with a decrease in the viable cyst population, but this should only occur when the cyst population is high and the eelworm population of the host plants is near saturation point." It is concluded that in the areas where the experiments were carried out, satisfactory potato crops can be grown provided that other conditions are favourable, even if the cyst population is high, i.e. over 25 per 10 c.c. of soil. If the initial viable cyst content is low, it will be considerably increased by the growth of a potato crop.

In Germany also many different chemicals have been tested for the control of the disease. Reinmuth (1929) used bone oil applied to the soil after a green crop had been ploughed in, and claimed to obtain an increase in yield of potatoes and a decrease in cyst content of the soil. Goffart (1943a) considered the use of various chemicals, but came to the conclusion that none are of any great practical use.

Among the most recent published works on methods of chemical control of the potato root eelworm are those of Chitwood & Buhrer (1945), Chitwood (1946), the United States Department of Agriculture (1946a,b), Robertson (1947), Martin (1947), Schmitt (1948), Peters (1948a,b), and the United States Bureau of Entomology & Plant Quarantine (1948). No complete eradication of the eelworm is claimed, but very considerable reduction in its numbers may be achieved. Chitwood & Buhrer had the most promising results with various methyl bromide mixtures, and with chloropicrin, carbon disulphide, and D-D mixture (two parts of 1,3-dichloropropylene and one part of 1,2-dichloropropane). In assessing the efficacy of the various treatments, they took into account the cost of the treatment and the value of the increase in crop resulting from it. The most profitable treatments were carbon disulphide at 1,000 lb. per acre and D-D mixture at 500–860 lb. per

acre. Although chloropicrin gave increased yields of potatoes, and at some doses a considerable reduction in the numbers of nematodes, its cost was in all cases too great to be offset by the increase in yield. The three methyl bromide mixtures tested were Dowfume E (90% ethylene dichloride, 10% methyl bromide), Dowfume P (90% propylene dichloride, 10% methyl bromide) and Dowfume G (67.5% ethylene dichloride, 22.5% carbon tetrachloride, 10% methyl bromide). Although they were quite effective, the cost of treatment was repaid in very few cases.

In 1946 Chitwood gave the results of tests of D-D mixture at various doses up to 1,700 lb. per acre applied by hand, and up to 1,213 lb. per acre applied by machine. With hand applications he claims odds of 99 to 1 that the treatments were better than 98% and 99% effective for doses of 850 and 1,700 lb. respectively on plots surrounded by uninfested soil. On plots surrounded by other infested plots the odds were that hand treatments were better than 94, 95, 96 and 96% effective for doses of 425, 675, 850 and 1,275 lb. per acre respectively. Machine application of the chemical was less effective, but the odds were 99 to 1 that the efficacy was always above 86%. Under the conditions of the experiment this chemical showed promise as a lethal agent for *H. rostochiensis*.

D-D mixture was also used by Robertson (1947) in a glasshouse where tomatoes were badly attacked by both *H. rostochiensis* and *H. marioni* (the root-knot eelworm). He applied it in holes 8 in. deep and 12 in. apart at the rate of 400 lb. per acre, and found that the plants grew much better and gave bigger yields on the treated than on the untreated ground. Very few cysts were found on the roots, and the cysts which remained in the treated soil contained only 65% of viable eggs as compared with 96.5% in the untreated soil. Martin (1947) found D-D mixture to be more effective in sandy than in peaty soils. Schmitt (1948) tested allyl bromide, D-D mixture, trimethylene bromide, ethylene bromide, ethylene dibromide, and Iscobrome-D in pots, and although all had some lethal effect on the cysts at 23 gal. per acre, only the last two, when applied at the rate of 76 gal. per acre, completely eradicated the nematode. D-D mixture was applied 6 in. deep at the rate of 450 lb. per acre to 1,557 acres infested with potato root nematode in Long Island during 1946 (United States Bureau of Entomology and Plant Quarantine, 1948), but the results of the treatment are not given. D-D mixture at the rate of 1,460 lb. per acre was shown by

Peters (1948a,b) to have a beneficial effect on potatoes grown in pots of soil to which it had been applied, even in the absence of potato root eelworm.

In addition to using chemicals for the purpose of killing the nematode in the soil, certain substances have been tested with the idea of inhibiting or retarding the hatching of the larvae, so that the potatoes may at least get a good start before being attacked. It was thought that ferric oxide might be useful for this purpose, since there was evidence (Hurst & Triffitt, 1935a ; Carroll & McMahon, 1937) that it caused inactivation of root diffusates, with consequent retardation of hatching of eelworm larvae. When tested in a small-scale field experiment in one locality (Hurst & Triffitt, 1937), an application of ferric oxide to the soil resulted in increased yields of potatoes, but in other places (Hurst & Franklin, 1937, 1938a) no benefit was observed, and the use of this chemical has been abandoned.

Root diffusates of certain cruciferous plants appear to have the effect of retarding or inhibiting the hatching of potato eelworm larvae (Triffitt, 1929a, 1930a ; Ellenby, 1945a). The effect usually seems to pass off when the treated cysts are removed from the cruciferous root diffusates to potato root diffusate. Observation of this behaviour led Ellenby (1945b,d) to test solutions of allyl isothiocyanate (mustard oil), which is probably the substance concerned. In a small-scale field trial on eelworm-infested soil, greatly increased yields of potatoes were obtained when 3 c.c. of allyl isothiocyanate in a gallon of water was absorbed on about 4 lb. of coarse peat and applied to each 10-foot row of potatoes at planting time. No information is given as to the numbers of cysts on the roots of the plants at the end of the season in either the treated or control rows. It is stated that the yield was increased by about 100% in some cases.

Goffart (1941d) states that he has found a chemical (referred to by a number) which prevents hatching of *H. rostochiensis* larvae at a concentration of 0.001%, and is nematocidal at higher concentrations. When it was used at 100–150 gm. per square metre very few cysts were formed on potato roots.

It seems likely that at least some of the chemicals which have given improvement of the crop on "potato-sick" land owe their efficacy in some degree to their action in partially sterilizing the soil. It was shown by Carroll & McMahon (1935) that in soil

sterilized by heat, potato root diffusate fails for a time to stimulate eelworm larvae to hatch. If chemical sterilization of the soil has the same effect, this fact coupled with the fertilizing properties of the chemicals might account for the healthy growth of the potatoes, even when they are heavily attacked by nematodes.

One of the substances which may act in this way is formalin, which was found by Ogilvie (1934) to result in increased yields of potatoes when it was watered on to infested land before the seed was set. Mercuric chloride was tested by Johnson (1936) who found, in small field trials of this chemical on infested land, that the potato crop from treated plots was increased and that the plants bore few cysts as compared with the controls. In addition, there was only a slight change in the cyst content of the soil as compared with a considerable increase in cyst numbers on the control plots, but the same number of cysts from the treated plots seemed to be viable after treatment as before. This points rather to a temporary prevention of hatching than to a lethal effect on the cysts.

Amongst other substances which have been found in laboratory experiments to be to some extent lethal to cysts, but which have not all been tested on a field scale and in some cases are not suitable for use in the soil, are silver proteinate, silver benzoate and silver lactate (Boyd, 1943b), which appear to be lethal in solutions of 0.01–0.05% ; sulphur dioxide (Fenwick, 1942a) ; hypochlorites, chloroacetates and phenyl isothiocyanate (Smedley, 1936, 1938, 1939). A proprietary preparation called " Cystogon " was found by Goffart (1941c) to be of some benefit in field trials, and Ellenby found that allyl isothiocyanate applied to small plots of " potato-sick " land substantially improved the potato crop (1945d, 1946b).

Induced Hatching of Larvae.—Some chemicals seem to have the property of stimulating larval hatching at low concentrations, particularly the hypochlorites (Smedley, 1936) and silver compounds (Boyd, 1943b). They have, however, never been employed successfully on a field scale against *H. rostochiensis*. Triffitt (1932a, 1934) found that hatching could be induced on a field scale by growing the grasses *Poa pratensis* and *P. trivialis*. In experiments by Franklin (1937a) the cultivation of maize on eelworm-infested land appeared to result in a greater degree of emptying of the cysts than did the growth of lupines.

More recently Todd *et al.* (1947) have shown that anhydrotetronic acid is very active in causing larvae to hatch from the cysts : its

chemical structure is described by Marrian, Russell, Todd & Waring (1947).

Another means of emptying the cysts, and at the same time trapping and destroying many of the free larvae, is with trap-crops of potatoes. This method of reducing the infestation of a soil was tested by Carroll & McMahon (1937, 1939) and was found to be effective to some extent, provided that certain conditions were observed. In practice it could probably only be applied on a small scale, on account of the labour required in removing the potato roots. In methods of control involving the hatching of larvae from the cysts in the soil, and also to some extent after growth of an ordinary crop of potatoes in infested soil, numbers of free larvae will probably be left behind. It was shown by Franklin (1937b) that free larvae of *H. rostochiensis* may survive in the soil for as long as sixteen months under sheltered conditions, so that this possibility must be borne in mind in planning a crop rotation and in practising trap-cropping. It was shown by Carroll & McMahon that it is quite useless to follow a trap-crop removed early in the season with a crop of late potatoes, however thoroughly the trap-crop is removed.

Preventing the Development of Disease Symptoms.—In spite of all the work which has been done in attempts to control the potato eelworm by chemical means, no cure has been devised, and all that can be recommended are palliative measures, chiefly designed to prevent the potatoes from becoming diseased rather than to prevent their infection by the nematode.

It has been found that various chemical fertilizers applied to the soil, while apparently not harming the nematode, enable the host plant to grow well and produce a good crop at least in the first year after the application of the dressing. Blenkinsop (1935) found that heavy dressings of potash greatly improved the growth and yield of potatoes on infested land in Devon and Cornwall, where it had become impossible to raise a crop. The soil in this case had a very unfavourable phosphate-potash ratio, and uninfested soils in the same area also benefited strikingly from additional potash. Other workers have found applications of nitrogen to be of value on "potato-sick" land. The improvement after dressings of calcium cyanamide is probably often due, at least in part, to the additional nitrogen in the chemical (Walton, Ogilvie & Brian, 1936). It was shown by Walton, Ogilvie & Hickman (1937) that the percentage of nitrogen in the young leaves of affected potato plants growing on

" potato-sick " land was constantly lower than in apparently healthy plants. They concluded that eelworm attack had, at least in this case, upset the normal nitrogen metabolism of the plants. Goffart came to rather a similar conclusion when (1938a) he observed that the " factor of depression " which plays a part in eelworm disease of potatoes, and which is probably a metabolic upset, can be mitigated by increasing the supply of nitrogen.

A suggestion was put forward by Ellenby (1942) that the unknown factor causing disease in potatoes growing on eelworm-infested land might be a deficiency of some trace element essential to the healthy growth of the plants. He attempted to test this hypothesis by growing potatoes on " potato-sick " land and watering them with dilute solutions containing boric acid, zinc sulphate, manganese chloride, calcium sulphate and salts of cobalt and nickel. Each salt was applied to a single row of fifteen plants, and in each row three different concentrations of the salt solution were used, each concentration being applied to five consecutive plants in the row. The heights of the plants and crop weights were measured, and in general ran parallel. For each salt the mean height of the five plants which had received the strongest solution was greater than that of the other plants, while the shortest were those which had received the weakest solution. In most of the rows, especially those receiving boron, zinc or manganese, the treated plants grew better than those in the adjacent untreated rows. The experiment was of a preliminary nature, but no other work along these lines has since been published.

Farmyard manure has been found beneficial in some areas of bad potato sickness. O'Brien & Prentice (1930) quote one instance of a heavily infested field which in 1929 received a dressing of dung equal to 15 tons per acre, after which a crop of potatoes was grown. The following year one half of the field again had 15 tons per acre of dung, applied in the drills, and the other half of the field had 12 cwt. per acre of a complete artificial fertilizer. Kerr's Pink potatoes were grown and yielded a crop equal to 6 tons 3 cwt. per acre on the dunged half of the field and 1 ton 11 cwt. per acre, with no ware-sized tubers, on the other. There was no decrease in the cyst numbers in the soil.

The obvious, simple measure which can be applied to " potato-sick " land, and which usually results in a temporary improvement, is the withholding of potatoes for a number of years (Miles & Miles,

1946). In cases of bad sickness at least four or five years are required before a reasonably healthy crop can be expected, i.e. not more than one crop every four or five years will have any success on infested land, and the nematodes which die out in the soil during the intervening years will certainly be replaced in the season in which the potatoes are grown. Since only potatoes and tomatoes are infected by *H. rostochiensis*, apart from one or two weeds which are doubtful hosts, any other crop may be grown in the rotation. Certain grasses and maize, and possibly other plants, apparently cause more emptying of the cysts than do the more usual crops, but provided that volunteer potatoes and tomatoes are not allowed to grow the choice is (at any rate theoretically) unrestricted.

Resistant Varieties of Potato.- Search has been made by several workers for varieties of potato which might be immune, or at least resistant, to nematode invasion, or which could be guaranteed to remain healthy if grown on "potato-sick" land. O'Brien & Prentice tested twenty-seven varieties for three years in badly infested soil, and found evidence of resistance in some of them, but they give no details as to the degree of resistance or how it was estimated. Goffart (1934a) tested fifty-two varieties of potato but found no resistance in any. In his paper published in 1939 (d), he describes intensive trials which he conducted on a number of varieties. He grew the plants for 8–12 weeks in heavily infested sandy soil kept warm and moist in a greenhouse. When the female worms were showing clearly on the roots the plants were very carefully dug, and the white and yellow cysts counted. In the first year of the trial the growth of the plants was evaluated and the cysts on the roots counted : the trial was repeated in the following year, and this time the cysts on a single long root were counted and the average on 10 cm. of root was calculated. The varieties were then grouped according to the observations. Goffart concluded that most varieties varied considerably from plant to plant and often show variations in resistance from year to year, and there appeared to be no direct relationship between plant health and nematode attack, some varieties showing considerable damage when apparently only lightly attacked. He therefore concluded that varieties must be tested over several years and under various field conditions before their degree of resistance can be determined. Most early varieties he found to be not worth cultivating on eelworm-infested land, while others deteriorate quickly. He lists forty which are unsuitable for

" potato-sick " soil. He found only seven with a limited resistance, and no strong resistance in any variety. He also tested twenty-two of the same varieties tested by O'Brien & Prentice, but obtained rather different results. This supports his view that resistance depends a great deal on local conditions. Reinmuth & Engelmann (1940) compared the effects of nematode attack on a first early and a second-early potato (" Juli " and " Ackersegen ") and found that the effects were linked with factors such as temperature and rainfall, upon which the development of the roots was to a large extent dependent. The course of development of the plants depended on temperature rather than on nematode attack, but the yield was affected by the parasites as well as by nutrition and by soil moisture.

In 1939 Robertson published figures for the yields from eight varieties of potato grown for nine consecutive years on a plot in Aberdeenshire which had become heavily infested with eelworm, and from five of the same varieties grown for one year on " potato-sick " soil in Lincolnshire. In both cases Epicure, an early potato, yielded best of all the varieties (Goffart, 1939d, had also found that Epicure was one of the best croppers on infested soil, but O'Brien & Prentice, 1930, class it amongst the ' still less resistant " varieties), and Kerr's Pink was the best late variety. The cyst burden on the roots of the more successful varieties showed no difference from that on the more severely diseased ones, and no explanation of the apparent tolerance of Epicure and Kerr's Pink could be offered.

Gemmell (1943) tested the varieties Epicure, Doon Star, Majestic and Golden Wonder by growing them in pots of sand, to each of which had been added 20,000 larvae. When the plants had matured and died down the cysts produced on their roots were counted, and samples of the cysts were measured and tested for viability. Gemmell found that fewer cysts were produced on the roots of Epicure and Doon Star than on Majestic and Golden Wonder, the average number per plant being approximately 468, 576, 882 and 1,134 cysts per plant respectively for the four varieties. He also found that the mean size of the cysts was less on Epicure and Doon Star than on the other varieties, and that in extended laboratory tests the average number of larvae hatching from each cyst and the proportion of cysts which produced larvae were both smaller for cysts from Epicure and Doon Star than for cysts from Majestic and Golden Wonder. Gemmell therefore concluded that the varieties

Epicure and Doon Star exhibit definite resistance to the unhindered development in their roots of *H. rostochiensis*, as compared with its development in Majestic and Golden Wonder. The way in which this resistance is brought about is not understood. Ellenby (1946a) in more elaborate tests, and treating his results statistically, obtained similar results to those of Gemmell as regards the size and viability of the cysts from the varieties Epicure and Doon Star, but does not agree with the conclusions drawn by Gemmell.

More recently Mai & Lownsbery (1948) have tested thirty-four varieties of cultivated potato in eelworm-infested soil, but none showed any resistance. They also tested six tomato varieties and compared them with sixteen of the potatoes, and found that the tomatoes were less strongly attacked than the potatoes, but that there was no difference in degree of attack among the tomatoes.

Further search for varieties of *Solanum* which might be resistant to *H. rostochiensis* has been made by Hawkes (1945) and by Ellenby (1945), who tested a number of wild tuber-forming species from America in the hopes of finding one suitable for breeding a resistant cultivated variety. Ellenby tested about forty species in duplicate in infested soil ; in only one case, *S. pampasense*, were no cysts found. In some other species the cysts were noticeably fewer or slower to mature than those on the roots of Great Scot plants grown under the same conditions. In hatching trials, root diffusates from fifty-six South American species of *Solanum* generally caused fewer larvae to emerge from potato root eelworm cysts than did diffusates of *S. tuberosum* var. Great Scot ; two of the South American species stimulated no emergence at all. A comparison was also made of the viability of the cysts borne on the South American species *S. calcense* and on Great Scot. Although the cysts did not differ significantly in size, *S. calcense* cysts produced fewer larvae and there was a greater number of cysts from which no larvae could be induced to hatch than from Great Scot. Ellenby concluded that there was evidence of some degree of insusceptibility in some of the South American forms ; neither he nor Hawkes found any entirely immune variety, but *S. hallsii* proved exceptionally resistant (Ellenby, 1948). Tests (unpublished) by Smedley at the Institute of Agricultural Parasitology, St. Albans, on a number of varieties of potato from Peru gave no evidence of complete resistance, but some plants bore fewer and smaller cysts than others.

As far as is at present known, therefore, there seems to be little

hope that any of the cultivated or the known wild varieties and species of *Solanum* are likely to prove immune to *H. rostochiensis*, though varieties may in time be developed capable of producing good yields in spite of eelworm attack (Anon., 1941c). For example, Chitwood & Buhrer (1946a,b) found that the variety Irish Cobbler made good root growth at temperatures of 45°–58° F., which is below the temperature at which mass invasion by the eelworm larvae takes place. On the other hand, Green Mountain makes little growth below 54°–58° F., which is not far below the temperature at which the larvae are most active. In a season in which there is a prolonged period with temperatures of 45°–55° F., Irish Cobbler will therefore probably grow quite well in infested soil, while Green Mountain is likely to do badly.

Reinmuth & Engelmann (1941) tested thirteen tomato varieties for susceptibility to *H. rostochiensis*, but found no very marked resistance in any.

Prevention of Spread.—While the origin in Britain of *H. rostochiensis* can only be guessed at, since it is a parasite very seldom observed on any native plant and is highly adapted to two cultivated plants of comparatively recent introduction the means by which it is introduced to new areas are obvious. In the resistant brown-cyst stage the nematode is very readily blown by the wind or transported over short distances in lumps of soil on farm implements of all descriptions, as well as on the feet of man and animals and by cultivations. It is also very easily carried on seed potatoes (Wellington, 1938), which are never entirely free from adhering soil, and if these have been grown in infested ground the parasite is introduced with them wherever they are planted. In this way, if no precautions are taken, the nematode may spread wherever potatoes are grown. For this reason, some attempts have been made to develop a practical method of ridding seed potatoes of soil and cysts by washing (Leiper, 1940a,b), or of killing the adhering cysts by fumigation (Fenwick, 1942a) or by soaking in formalin solution (Franklin, 1939b, 1940b). Machmer (1946) developed a combination of dry brushing and jet-washing, and further methods of cleaning seed potatoes are described by the United States Bureau of Plant Industry, Soils and Agricultural Engineering (1948), the most promising being that of dipping the tubers for five minutes in a 0.5% or a 1% solution of ammonia at 110° F.

Treatment of tubers with warm water alone has not been fully

investigated, but Triffitt & Hurst (1935) found that for cysts isolated from soil and immersed in hot water, temperatures of 116° F. for forty-five minutes and 118° F. for fifteen minutes were lethal, while Engelmann (1942) found that in dry soil a temperature of 60°–70° C. (140°–158° F.) for twenty-four hours was necessary to damage the cyst contents, and in wet soil temperatures above 50° C. (122° F.) were necessary. Below the lethal temperatures the larvae seemed to be somewhat stimulated. It seems unlikely that warm water alone will be of use for disinfecting seed potatoes, since the tubers would probably be damaged at the temperatures needed to kill the cysts.

There is thus no entirely satisfactory means known as yet for ridding seed potatoes of adhering eelworm cysts.

Legislative Measures.—In Northern Ireland (Patterson, 1948), Germany (Ext & Goffart, 1937), Sweden (Ahlberg, 1933), and the U.S.A. (United States Department of Agriculture, 1944; McCubbin, 1946, 1948), strict regulations and quarantine measures are enforced in order to prevent the spread of *H. rostochiensis*.†

Hosts

The only certain hosts of *H. rostochiensis* (with one exception) are members of the Family Solanaceae. Other plants have been recorded as bearing cysts of the potato root eelworm, but these records were made before this species was clearly recognized as being distinct from the sugar-beet eelworm, and the possibility of the presence of other cyst-forming species of *Heterodera* was therefore not taken into consideration. For this reason Morgan's (1925) record of the infection of *Chenopodium album* by the potato root eelworm is of very doubtful validity, since this plant is known to be infected by eelworms forming cysts like those of *H. schachtii* found on sugar-beet (Petherbridge & Jones, 1944), and Morgan does not appear to have examined the shape of the cysts which he found.

Mai & Lownsbery (1948) tested 171 species of flowering plants, but only potatoes and tomatoes became infected, the latter significantly less strongly than the former.

† Quarantine measures have more recently been adopted in Holland, and the certification of seed potatoes from growing crops which are free from visible infestation with potato root eelworm has been introduced in Scotland.

H. rostochiensis is known to be capable of infecting the following plants :—

SOLANACEAE

Solanum tuberosum (potato)—very heavily infected

Lycopersicon esculentum (tomato)—very heavily infected

Solanum dulcamara (woody nightshade or bittersweet)—lightly infected (Morgan 1925 ; Franklin 1940a)

Atropa belladonna (deadly nightshade)—lightly infected (Franklin 1940a) ; not infected (Triffitt 1929d)

Solanum nigrum (black nightshade)—infected (Vañha & Stoklasa 1896) ; Franklin (unpublished) found many larvae in the roots but no cysts later

Solanum sarachoides = *S. chenopodioides* Lamarck (a weed introduced into Britain in carrot seed from South America)—heavily infected in pots but not yet found infected in the field (Bates 1945)

Hyoscyamus niger (henbane)—infected (Vañha & Stoklasa 1896) ; not infected (Triffitt 1929d)

In addition, a large number of South American species of *Solanum* tested by Ellenby (1945c) were found to bear cysts. Triffitt (1929d) had negative results in tests of eight other solanaceous plants.

SCROPHULARIACEAE

Antirrhinum majus (snapdragon)—seen once by the writer bearing round golden-yellow cysts, probably *H. rostochiensis*

DISTRIBUTION

H. rostochiensis is very well known in most of the countries of north-western Europe, and has been recorded from Britain, the Channel Islands, Germany, Denmark and Sweden. It has recently (1941) been recorded from a single area on the North American continent, namely Long Island, New York (Cannon, 1941).

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